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THE FUNCTIONAL SIGNIFICANCE OF THE ARRANGEMENT OF THE CEREBRAL AND CEREBELLAR VEINS

By JOHN S. B. STOPFORD, F.R.S.

During a study of the Great Vein of Galen (1, 2), my attention was called to certain facts in connection with the veins draining blood from the cerebral hemispheres and the cerebellum. The points raised in this paper are the outcome of a fuller investigation of these facts and their interpretation.

It has long been known, and almost every anatomical text-book stresses the fact, that the superior cerebral veins open obliquely into the superior longitudinal sinus, and that their direction is opposed to that of the current of the blood in the sinus. Only a few books, however, attempt to give a reason for this arrangement, although at least three explanations have been offered at various times. In the first place, it has been suggested that this curious mode of termination in the sinus provides one of the factors which prevents sudden depletion of the cerebral veins in consequence of the inspiratory emptying of the large intracranial venous channels. Secondly, it has been pointed out that the arrangement prevents regurgitation of blood from the sinus into the cerebral veins: and thirdly, Symington (3) denied any functional significance and expressed the view that the obliquity of the superior cerebral veins appeared to be merely secondary to the backward growth of the cerebral hemispheres.

It is difficult to agree with Symington's suggestion that the arrangement has no functional importance when the investigation is extended to other veins draining the blood from the brain into the cerebral sinuses. A closer study of their structure and precise course, in the light of recent knowledge regarding the relative pressures of blood in the sinuses and the cerebro-spinal fluid, does seem to indicate that the arrangement serves a most important and useful physiological purpose.

CEREBRAL AND CEREBELLAR VEINS

At the outset, attention was directed to the superior cerebral veins, but as certain facts emerged the investigation was extended to the other veins conveying blood across the subarachnoid space from the various parts of the brain to the intracranial venous sinuses.

It was found that the number of superior cerebral veins opening into the superior longitudinal sinus was smaller than usually described, only four or five being observed on each side as a rule. These may be named, as Sargent (4) has proposed: Frontal, Precentral, Postcentral and Occipital. The smaller

Frontal commonly approaches the sinus at a right angle, but the others invariably extend forwards and inwards to open against the current. All these veins after crossing the subarachnoid space, run for a distance of about half-an-inch in the substance of the dura mater as usually stated: in this part of their course they may pass under a lacuna, but my observations confirm those of Le Gros Clark (5), in that the veins never discharge their contents into a lacuna but always open into the sinus direct. It is noteworthy that the meningeal veins, which of course do not cross the subarachnoid space, do not usually follow this oblique course and commonly open into the lacunae. The orifices of the superior cerebral veins in the sinus are so constructed and placed that they are maintained in a widely open condition when the sinus is filled with blood, in fact, they do not appear to collapse when the sinus is empty. The wide-open entrance to the veins has been demonstrated by several observers, who have found that fluid injected into the sinus from behind runs with the greatest readiness into the cortical veins, and by some, this observation has been used as an argument against the assumption that the obliquity has any functional significance.

Histological examination of sections of the veins, as they cross the subarachnoid space and as they extend to the sinus in the substance of the dura, reveals further points of interest. The thinness of the venous wall is well known, but the most remarkable feature in their structure is the reduction, when compared with veins from other regions, in the amount of muscle. Whilst traversing the subarachnoid space, the muscle coat forms only a very thin internal ring, which is surrounded by a fibrous layer forming about seven-eighths of the whole thickness of the wall. When the vessels pierce the dura, the muscular coat is still more insignificant, is even difficult to recognise without a differential stain, and does not always form a complete layer. In other words, the terminal part of the superior cerebral veins has a wall very similar to that of the sinus, and in this part of their course the veins may be considered as patent tubes, with fibrous walls outside the endothelial lining, which are extensions of the sinus.

Such an arrangement and structure do seem to infer a functional bearing, and this deduction is enhanced when reference is made to other veins entering the venous sinuses from the brain. My own observations make it evident that all the larger veins which cross the subarachnoid space have walls similar in structure to those just described, and enter the sinuses in the same manner. Their course in the substance of the dura may not always be of the same extent as that stated with regard to the superior cerebral veins, but the fundamental arrangement, in the case of those of sufficient size to make a satisfactory dissection, is the same.

THE PRESSURE OF THE CEREBRO-SPINAL FLUID AND THE BLOOD IN THE VENOUS SINUSES

From a large series of experiments the researches of Weed and Hughson (6) have demonstrated that in almost every case the pressure of the cerebro-spinal fluid was considerably higher than that of the pressure of the blood in the hinder part of the superior longitudinal sinus. The results of the work of Weed and Hughson confirmed the views of Dixon and Halliburton (7), who fifteen years ago had corrected the opinion expressed by Leonard Hill (8) that the cerebro-spinal fluid and cerebral venous pressures were the same. Consequently it seems to be established definitely that the cerebro-spinal fluid pressure is normally above that of the pressure in the intracranial sinuses. The venous sinuses possess strong walls and can withstand the pressure, but the veins which cross the subarachnoid space, where they are fully exposed to the cerebro-spinal fluid pressure, have thin walls. From the foregoing it is clear that these veins would collapse under the pressure exerted from without by the cerebro-spinal fluid if the pressure within them was no greater than that in the sinuses. This fact seems to have escaped recognition until it was appreciated by Brain (9), who pointed out that it is not legitimate to assume, as has been done, that the pressure in the cerebral veins is as low as that in the large intracranial sinuses. It is evident that the pressure in the veins crossing the subarachnoid space must be sufficiently high to withstand the pressure of the surrounding cerebro-spinal fluid, and I suggest that the arrangement described in this paper provides the mechanism by which the pressure in these veins is maintained above the level of that in the sinuses. The flow of blood in the sinuses passing the open orifices of the veins, which approach the sinuses against the current, will obviously impede the discharge of blood from the veins into the sinuses and so raise appreciably the pressure within the former. The fibrous nature of the wall of the veins, with a very meagre amount of muscle as they approach the sinus, is quite in accord with such a mechanical device. Such an arrangement will ensure that the pressure in the veins is probably sufficient, under normal circumstances, to enable them to withstand the cerebro-spinal fluid pressure. Conditions which prevail under abnormal circumstances are of clinical interest and reference must be made to them.

Whilst it is now well known that there is a relationship between arterial, venous and cerebro-spinal fluid pressures, there is also no doubt that the latter must be considered as more independent of the other two than was formerly believed. Evidence has been submitted to show (6, 10, 11) that the fluid pressure may be altered independently of any change in the intracranial and systemic vascular pressure. Consequently under abnormal circumstances, as an excessive production of cerebro-spinal fluid or serious interference with its absorption, the fluid pressure may be raised very considerably above the pressure in the sinuses. In such abnormal conditions the fluid pressure may be so raised as to compress or cause collapse of the veins crossing the subarachnoid space

and so induce venous congestion of the nervous tissue. It appears probable that this is the cause of the venous engorgement of the cortex seen not uncommonly at post-mortem examination of cases which have suffered from a moderate degree of raised intracranial pressure. Elsewhere (1, 2) I have submitted evidence which strongly suggests that, in many patients suffering from raised intracranial pressure secondary to growths within the skull, the primary cause of the elevation of pressure is due to compression of the Great Vein of Galen. Such compression impedes the venous drainage from the choroid plexuses, raises the capillary pressure in these structures, and produces an increase in the production of cerebro-spinal fluid. The increased amount of cerebro-spinal fluid may escape from the ventricular system into the cisternae and general subarachnoid space, provided there is no obstruction at any point, and be insufficient to cause any very obvious dilatation of the ventricles. In this case the pressure in the subarachnoid space may be raised sufficiently to impede the drainage by the cerebral and cerebellar veins and so lead to a venous engorgement. If the increased production of cerebro-spinal fluid is greater in amount, the ventricles are liable to be dilated, the aqueduct being too narrow to provide an escape of the fluid at the same rate as its production, i.e. a relative obstruction—and in consequence the nervous tissue of the cerebral hemispheres is pressed against the resistant walls of the skull. This will interfere with the circulation of the cerebro-spinal fluid over the hemispheres, and will limit absorption, which in turn leads to an exaggeration of the already raised intracranial pressure. In such cases of greatly elevated intracranial pressure, the effect of the dilatation of the ventricles and compression of the nervous tissue against the membranes and bones is to produce the characteristic flattened and anaemic condition of the cortex seen so frequently post-mortem, after a pronounced rise of intracranial pressure. The flattening and pallor of the cortex is always associated with and recognised by the pathologist as an expression of internal hydrocephalus.

In this way the opposed post-mortem findings in cases exhibiting raised intracranial pressure of venous engorgement of the cortex or anaemia associated with varying degrees of flattening become intelligible.

SUMMARY

1. All the veins traversing the subarachnoid space pass obliquely to the intracranial sinuses, so that their course is opposed to the direction of the current of blood in the sinuses.

2. The orifices of these veins are so constructed and arranged that they are permanently open.

3. Sections of the veins as they cross the subarachnoid space and pierce the dura show their walls to be very thin and almost entirely composed of fibrous tissue.

4. It is suggested that this arrangement and structure have a functional

significance, and served to raise the pressure in the veins and prevent their collapse by the pressure of the cerebro-spinal fluid surrounding them.

5. Reference is made to the influence of elevated intracranial pressure upon these veins.

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THE EARLY DEVELOPMENT OF THE FERRET: THE PRONUCLEI

By DONALD MAINLAND, M.B., Ch.B. (Edin.)
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Embryological literature contains numerous studies of the pronuclear stages of mammalian ova, and the addition to this collection of a report of any considerable size necessitates a word of explanation. The investigations communicated herein were carried out on the ova of the ferret, both of the light coloured and of the dark or "polecat" variety. The ferret belongs to the Carnivore group, and in this group no very complete study by modern methods of the transformations of the pronuclei has previously been carried out. In the second place, the application of statistical methods to a study of this type of specimen has apparently never before been attempted. Finally, in the present records emphasis has been laid on the influence of histological technique in the production of the phenomena observed in the specimens. The statistical treatment of the results of varying techniques in histology is still largely an unexplored field.

MATERIAL AND METHODS

From 30 different ovaries and 19 different animals 101 ova were examined. The animals were kept in captivity and fed on a mixed diet of bread, biscuit, milk and flesh. They were inseminated by the male while they were in oestrus, and were killed at a selected time after mating. The specimens (ovaries with uterine tubes or uterine tubes alone) were fixed, some in Zenker's fluid, others in strong Flemming's fluid, others in Perenyi's fluid, a few in Mann's fluid and a few in Mann's fluid with formol. Paraffin sections were prepared in series at 10 microns. The staining methods were Heidenhain's iron-haematoxylin with eosin or orange G; in other cases Mayer's haemalum and eosin. Most of the Flemming-fixed specimens were tinted with eosin. All the available Flemming-fixed ova were not chosen for examination because their lack of staining did not permit much detail of pronuclear structure to be demonstrated. This absence of random sampling had to be taken into consideration when statistical methods were applied, for random sampling is essential in statistical work. All the other available ova were chosen, except a few badly fixed specimens and a few specimens in which a fair number of sections was lost.

As will be subsequently seen, all the ova observed were not at the pronuclear stage; some were at the polar spindle stage and some at the stage of the first segmentation. The actual numbers of pronuclei taken into consideration are recorded in the appropriate sections below. In all, 71 out of the 101 ova were at the pronuclear stage of development.

STATISTICAL METHODS

In biological work it is becoming more and more widely realised that any phenomena that are capable of enumeration are capable of statistical treatment, and that any proofs based on these enumerations, unless they are statistical proofs, are unsatisfactory. A large part of the present investigations has involved the employment of one of the simpler statistical tests, namely the Chi Square test. As the description of this test in several of the commoner manuals is a little difficult to follow without a greater experience of statistical methods than many investigators possess, it may not be out of place to show how the test has been applied in one of the instances in the present research.

The purpose of the Chi Square test is to demonstrate association or independence between two sets of events or phenomena, e.g. between the number of hours that have elapsed after insemination of the animals and the position of the pronuclei in the ova obtained from those animals; or between the type of fixative used and the size of the chromatin particles in the pronucleus. The former of these two examples will be considered in detail here.

The pronuclei in the ova of the present collection of ferret specimens can be arranged according to the position of the pronuclei in the ovum, whether central, peripheral, or sub-central (i.e. between the central and peripheral positions). At the same time the pronuclei can be arranged according to the number of hours that elapsed between the insemination of the animals from which the specimens were obtained and the killing of those animals. By use of this combined classification the Chi Square test can be employed to ascertain whether there is any significant association between the position of the pronuclei and the number of hours that elapsed between the insemination and the death of the animal. That such an association is bound to exist is undeniable, but the object of the present investigation is to determine whether the present series of specimens is adequate to demonstrate the association.

In Table II, p. 266, there are 21 non-central pronuclei out of a total of 65. The factors, whatever they were, responsible for the distribution of the pronuclei found in this series have operated so as to cause 21/65ths of the total to be non-central. There are 14 pronuclei in the time period (A). Unless some additional factor entered in, it would be expected that the proportion of non-central pronuclei in this group would be the same as in the series as a whole, i.e. 21 : 65. The number of non-central pronuclei in that case would be 21/65ths of 14, i.e. 4·523. This may be called the "theoretical" or "expected" number. The actual number of non-central pronuclei in the group (A) is 9, an excess of 4·477 over the theoretical number. It is natural to suppose that this excess is due to the fact that ova found earlier after insemination will be at an earlier stage of development than those found later. On the other hand, the difference might be due to chance—the accidental presence of an excess, which might not be found if the total number of pronuclei in group (A) were larger. To eliminate this possibility and to show whether there are also unexpected distributions

in the other groups, (B) and (C), the following operations are performed. The expected numbers of pronuclei for the other squares or "cells" are calculated as above, and are shown in Table III. The expected or theoretical number is lettered t and the actual number a. The difference $a - t$ is found. Some of these differences are negative and some are positive. The differences are then squared, a process that eliminates the negative sign and so enables the numbers to be added without their counterbalancing each other's effects. The squaring also gives weight to the larger differences. The squared difference is divided by the corresponding theoretical number and is thus expressed as a proportion of t, since a large difference might mean very little if t also were large. The sum of all the numbers thus obtained is called χ^2, the method being named the Chi Square method. If χ^2 is large it implies that there is a large discrepancy between the expected arrangement and the actual one, some factor or factors having entered in to produce an irregularity in the distribution. In the present instance the two phenomena, time and the position of the pronuclei, are correlated or associated. The arrangement found is not due to mere chance. It is necessary to have some standard by which to decide whether χ^2 is large enough to be significant. This decision can be made with the aid of such a table as Fisher's (1928) Table III. It is clear that with a larger number of squares or cells than those of Table II (p. 266) the value of χ^2 might be equally large and yet not be as significant as if it were the product of a few calculations. The significance is therefore dependent on the number of cells, exclusive, of course, of the squares containing the totals and those containing the headings. If the group (A) in Table II and the first two columns of Table III are examined, it will be seen that the total 14 has been used in the calculation of t, and has therefore influenced the resulting χ^2, and when this total is fixed and one cell, say the (A) N.C. cell, is filled with the number 9, the other cell, (A) C., must be filled with the number 5. Similarly if the total 21 is fixed and two cells in the column N.C. are filled, the number in the remaining cell is determined. In calculating n, based on the number of cells, this fact is taken into consideration, and n represents the number of cells that can be filled arbitrarily. It is spoken of as the number of "degrees of freedom" and is found by taking the number of rows and the number of columns, exclusive of headings and totals, subtracting one from each and multiplying the two together. In Table II, $n = 1 \times 2$. With n and χ^2 Fisher's Table III can be used to find P, i.e. the proportion of cases in which the value of χ^2 will be exceeded, or the probability that χ^2 shall exceed the given value. Thus if the actual number of cells in a Chi Square test is 4, $n = (2 - 1) \times (2 - 1) = 1$, and if $\chi^2 = 0{\cdot}455$, $P = 0{\cdot}50$, and the chances are equal that a greater value of χ^2 should be found in such a case. If there are 6 cells, $n = (2 - 1) \times (3 - 1) = 2$. If χ^2 then $= 5{\cdot}991$, $P = 0{\cdot}05$. The chances of this value of χ^2 being exceeded are 0·05 to 0·95 = 1 to 19. With this value of P (0·05) and with any lower values, χ^2 is taken as significant, for the probability is so small that it should be due to chance. With any higher value of P, χ^2 is considered insignificant. In the present case $n = 2$, $\chi^2 = 9{\cdot}26$

and therefore P is lower than any value in Fisher's table. Hence there is a definite association between the time after insemination and the position of the pronuclei.

For further detail regarding the Chi Square method reference should be made to Yule (1927), pp. 64 *et seq.*, and especially to Fisher (1928), pp. 75 *et seq.*

MEASURES OF DEVELOPMENT OF THE PRONUCLEI

In any embryological study it is most desirable to express stages of development ultimately in terms of time, rather than in terms of contemporary phenomena. To do this directly with mammalian ova is not easy. The event from which time periods are measured in the ferret specimens now under consideration is not the actual fertilisation of the ovum, but the insemination of the animal. Robinson (1918) has shown that ovulation in the ferret may occur at any time between $30\frac{1}{2}$ and $93\frac{1}{2}$ hours after insemination; and, as fertilisation takes place at a varying time after ovulation, the time of insemination is obviously an unsatisfactory initial point from which to measure development. In the present series of specimens this lack of precision is further increased by the fact that in some cases more than one insemination took place during the time when the male and female animals were caged together.

Since it is impossible to obtain directly any close relationship between the duration of development and the phenomena that occur in its course, an attempt may be made to relate certain of the phenomena to others which are known to possess a definite time-sequence. For example, it is known that ova that possess two central pronuclei are at a more advanced stage of development than those in which the two pronuclei are only half way between the periphery and the centre of the ovum, and these ova are in turn more advanced in development than those in which the pronuclei are peripherally placed. This phenomenon—migration of the pronuclei—may be taken as a scale by which to measure other phenomena, e.g. changes in the cromatin of the pronuclei.

It might be thought that with our present embryological knowledge the study of a series of ova from an animal such as the ferret which has not previously been so studied, would consist merely in observing the manner in which the new specimens fitted into series of developmental stages described for other Mammals. As can be seen from such articles as that of O. van der Stricht (1923), however, the Mammals already so studied differ from each other in details, and it is therefore clear that caution is necessary. This is especially obvious when it is remembered that in the Carnivore group, to which the ferret belongs, there has never been described in detail the sequence of changes observed in the pronuclei. In the present study the object is in the first place to ascertain how far the series of specimens shows correlation between the time after insemination and the actual stages of development as represented by the approach of the pronuclei to the centre of the ovum.

Table I. *Position of pronuclei arranged according to the number of hours after insemination.*

(The numbers represent ova.)

Hours after insemination	One present; peripheral	Both present; peripheral	One central; one peripheral	Both subcentral	One peripheral; one subcentral	One present; central	Both central	Totals
41	1	.	.	.	.	.	.	1
41½	1	.	.	.	1	.	.	2
41½	1	3	1	1	.	1	4	11
44½	.	.	.	1	.	.	.	1
47½	.	4	.	1	1	.	13	19
51½	.	.	.	.	.	.	2	2
53½	.	.	.	.	.	.	1	1
64½	.	3	.	.	.	.	12	15
68	.	.	.	1	.	.	.	1
76½	1	.	.	.	.	.	6	7
116½	.	.	.	.	.	.	5	5
Totals	4	10	1	4	2	1	43	65

Table I[1] shows the ova arranged according to the position of the pronuclei and the time that elapsed between the insemination and the killing of the animal. For the purpose of determining whether there was any correlation between the recorded time-intervals and the positions of the pronuclei the Chi Square method was employed.

Table II. *Association between the post-inseminal period and the position of the pronuclei.*

Hours after insemination	Pronuclei not central (N.C.)	Pronuclei central (C.)	Totals
(A) 41 –41½	9	5	14
(B) 44½–53½	7	16	23
(C) 64½–116½	5	23	28
Totals	21	44	65

Table II contains most of the figures from Table I grouped in a manner suitable for this determination. The resulting value of χ^2 is 9·26. From consultation of Fisher's (1928) Table III this is found to be highly significant, since $n = 2$, and therefore P is lower than any value in the table. Moreover, it will be seen from Table II that in the middle period of time (B) the proportion of ova with non-central pronuclei to those with central pronuclei is 7 : 16 (roughly 1 : 2), i.e. about the same as the ratio between the totals (21 : 44). In the earlier group (A) the number of ova with non-central pronuclei is

[1] In the collection of ova studied there were several specimens obtained from an animal 7 days after insemination and several obtained from another animal 9 days after insemination. While the exclusion of these in the investigations upon time which are recorded in the text may be open to criticism, the author feels justified in this selection by his experience of the mating of ferrets for the purpose of obtaining tubal ova.

greater than those with central, while the reverse is the case in the group (C) with a longer period after insemination. One is therefore justified in concluding that in this series treated as a whole the length of the post-inseminal period is a measure of the progress of development, but it should be noted that this does not necessarily apply to the comparison of individual specimens or to groups smaller than the whole series here considered.

Table III. *Details of the calculation of* χ^2 *from the data of Table II.*

Designation of cell	Theoretical number (t)	Actual number (a)	$a - t$	$\frac{(a-t)^2}{t}$
(A) N.C.	4·523	9	+ 4·477	4·431
(A) C.	10·16	6	− 4·478	2·116
(B) N.C.	7·106	7	− 0·430	0·025
(B) C.	14·89	15	+ 0·430	0·012
(C) N.C.	9·046	5	− 4·046	1·809
(C) C.	18·95	23	+ 4·05	0·865

In subsequent sections of this article the time after insemination is used as a possible measure of the progress of development of the ova; but where, for one reason or another, the series of ova is not exactly the same as in the test just made, it is not assumed without further investigation that the times recorded actually indicated development.

PRONUCLEAR CHROMATIN

(*a*) *Early transformations*

The course of pronuclear development after fertilisation in animals generally, consists, as is well known, in the approach of the two pronuclei to each other, their enlargement, the change of the chromatic material from a more or less uniform basiphilic mass to particles of various sizes, and the final transformation of this material into the spireme of the first segmentation spindle. In the mouse and rat, Kremer (1924) has recently laid stress on a preliminary aggregation of chromatin before the division of it preparatory to the formation of the first segmentation spindle.

In the earlier phases of development, the two pronuclei approach each other and migrate toward the centre of the ovum. Their position, therefore, may be taken as an indication of the degree to which they have developed, and thus be used in studying the transformation of the chromatin. Fourteen ova from the series under examination illustrate various degrees in the migration of the ovum, and a brief description of their pronuclei is given to indicate the range of possibilities in the process of transformation.

In one ovum (no. 11) two pronuclei were found in the peripheral part of the ovum, both stained a uniform dark blue with haematoxylin, one spherical in shape, the other more ellipsoidal. Two other ova (nos. 36 and 48) possibly represented earlier stages than this. They each showed a peripheral deep purple

mass, of irregular shape in the one, spherical and lobulated in the other. These masses, it appeared, might be stages in the conversion of the daughter chromosomes of the second polar spindle into the female pronucleus.

In one ovum (no. 9) both pronuclei were spherical and stained a uniformly deep purple; but while one was peripheral the other was placed between the periphery and the centre of the ovum. Migration had commenced before any visible change in the chromatic material had occurred. On the other hand, in one specimen (no. 7) both the pronuclei were peripheral and of spherical shape; but while one formed a ring with a pale centre and a faintly purple lobulated periphery, the other was a uniformly deep blue mass (fig. 4). In another ovum (no. 10) both the pronuclei were peripheral; one was a spherical homogeneous purple body, while the other showed lobules at its edge which were more deeply stained than was the centre. In ovum no. 13 the two pronuclei were peripheral and somewhat lobulated; one was almost uniformly stained, in the other the centres of the lobules were more faintly stained than were the outer parts. In several ova (nos. 21, 30, 91 and 97) the pronuclei were peripheral and either of spherical or of broad ellipsoidal shape, while the chromatin was in the form of globules and granules of various sizes. A reticulum was found in most of the last-mentioned pronuclei. Ovum no. 90 also belongs to this group, but a full view of its pronuclei was not obtained because it was obscured by a foreign body in the preparation. In ovum no. 43 one pronucleus was peripheral, the other had commenced to migrate towards the centre; both contained globules and granules of chromatin of various sizes. In ovum no. 15 one pronucleus was near the centre of the ovum, the other was still peripheral. Both showed chromatin in globular form (fig. 6). A possibility never to be overlooked is that in a small series like the present one it is difficult or even impossible to determine whether specimens are perfectly normal or not; but with this proviso it appears justifiable to summarise the course of development as follows.

The pronuclei pass from a condition of uniformly stained chromatic material to one in which this material is in the form of globules and granules of various sizes. The change, in at least some cases, occurs by way of an intermediate stage in which the periphery of the pronucleus is in the form of lobules more deeply stained than the centre. The change may occur while the pronuclei are still in the outer part of the ovum, but the pronuclei may commence to migrate to the centre of the ovum before the change occurs.

It will be noted that no attempt has been made in this section to distinguish the development of the male pronucleus from that of the female. A consideration of the differences between the two pronuclei is reserved for a subsequent section.

(*b*) *Size of chromatin particles*

After the pronuclei have come together near the centre of the ovum, there ceases to be any satisfactory criterion by which to determine whether they are at an early or a late stage of development. It has been shown that in this series there is an association between the position of the pronuclei and the

number of hours that elapsed between insemination and death; but one is not therefore justified in assuming that of any two ova the one obtained shortly after insemination is at an earlier stage of development than the other which was obtained later. The majority of the pronuclei in this series of ferret ova were centrally placed. This central stage is a later one than those already considered in which the pronuclei were either peripheral or sub-central. In the central pronuclei the chromatin was always in the form of granules and globules. Some pronuclei showed various sizes of particles—large, medium and small. Others were remarkable because of the large size of their chromatin masses; others showed no very large masses, but some medium-sized and some small; others showed chiefly small particles. These standards are not numerical, but represent in a rough way the differences between the pronuclei in this respect. The question then arises how far one can arrange in order these types so as to conform to the stages described by other authors. In such a study it is necessary to bear in mind the possibilities of: (1) transient alterations in the constituents of the pronuclei, not directly connected with the main course of their development; and (2) the different effects of different fixatives.

At first the pronuclei, central, sub-central and peripheral, were arranged according to the size of the chromatin particles under the four classes: (1) those in which the particles were of various sizes; (2) those in which large particles were specially noted; (3) those in which medium-sized particles were noted, large particles being absent; and (4) those in which small particles were most notable. The pronuclei were at the same time further grouped according to the time that had elapsed after insemination; for it has been shown that the time-intervals in this series considered as a whole correspond to a real progress in the development of the ova. The Chi Square test was applied to demonstrate any association between the time and the size of the chromatin particles. Only specimens fixed in Perenyi's or in Zenker's fluid were selected. Owing to the smallness of the numbers in some of the classes, groups were made as shown in Table IV. The results of this test ($\chi^2 = 13{\cdot}78$, $n = 1$; P much less than 0·01)

Table IV. *Association between time and size of chromatin particles.*

Hours after insemination	Pronuclei with particles of various sizes (V.)	Pronuclei with large particles, medium particles, small particles (L.M.S.)	Totals
(A) 41½–51¾	31	5	36
(B) 64¼–116½	16	20	36
Totals	47	25	72

show that there was a very high degree of association between the size of the chromatin particles and the time which had elapsed after insemination. In the later stages there was an excess of pronuclei in the cell marked "L.M.S." Analysis of the original data revealed that there were no pronuclei with large

particles in the earlier stages, whereas in the later stages there were many with large and many with medium-sized particles, but none with small particles. The conclusion indicated is that the excess of pronuclei in the cell "L.M.S." in the later stages is really an excess of pronuclei with large and medium-sized particles. A possible source of error in these results is the use of two different fixatives—Perenyi's fluid and Zenker's fluid. Another table (Table V)

Table V. *Association between time and size of chromatin particles, specimens fixed in Perenyi's fluid being excluded.*

(The lettering is as in Table IV.)

Hours after insemination	(V.)	(L.M.S.)	Totals
(A)	20	4	24
(B)	12	6	18
Totals	32	10	42

was prepared with the same time-groups and size-groups but with all the specimens fixed in Perenyi's fluid excluded. It will be noted that in one cell only four individuals are found. If less than five individuals are found in any one cell the tendency is for the association to become apparently significant; and therefore if less than five instances are found in any one cell and the association is not significant, the result can be accepted as in no way vitiated by the smallness of the number of instances. In other words, one can produce valid negative results even with less than five instances in a cell. In the present case, where specimens fixed in Perenyi's fluid were excluded there was no significant association between the time and the size of the chromatin particles ($\chi^2 = 1{\cdot}57$; $n = 1$; $P > 0{\cdot}20 < 0{\cdot}30$). A further application of the Chi Square test showed that there was a highly significant association between the size of the particles and the fixative (Perenyi or Zenker), for $\chi^2 = 5{\cdot}30$; $n = 1$; $P < 0{\cdot}05 > 0{\cdot}02$. This association was not so highly significant as that between time and size of particle. It was noted that the significance of the result was largely due to the proportions of the Perenyi specimens, which were equally distributed between the groups representing size of particles, whereas the proportions which held in the series as a whole were 47 with particles of various sizes to 25 with particles large or medium or small. From the original data it appears that this excess of Perenyi specimens in the second group is due to a preponderance of Perenyi specimens in which the particles were large.

Finally it was determined that there was no significant association between the time and the fixative ($\chi^2 = 2{\cdot}06$; $n = 1$; $P < 0{\cdot}20 > 0{\cdot}10$). Since this is so, there was obviously not a sufficient preponderance of Perenyi specimens in the later stages to account for the association between time and size of particle. Similarly the highly significant association between fixative and size of particle could not be accounted for by a preponderance of Perenyi specimens in the later group, where large and medium particles were more commonly found.

The results obtained in this section may be summarised as follows:

(1) There is a highly significant association between the size of the particle and the time after insemination (larger and medium-sized particles being found in later periods). This association exists only with specimens fixed in Perenyi's fluid.

(2) There is a highly significant association between the size of the particle and the fixative, Perenyi's fluid tending to give larger particles.

(3) There is no significant association between the time after insemination and the fixative. The specimens have therefore been chosen in a sufficiently random manner in this respect to render the results statistically sound.

It should be noted that these investigations on the size of the chromatin particles did not include all the specimens for which in an earlier section (p. 266) there was shown to exist a correspondence between the time after insemination and the development, as indicated by the position of the pronuclei. Before it could be definitely stated that there was any association between the development and the size of the particles, it would be necessary to prove this association either directly by reference to the position of the pronuclei in the specimens under consideration, or indirectly, by showing that in these particular specimens the time after insemination was a measure of the progress of development. Unfortunately the smallness of the series of specimens will not allow either of these methods to be employed.

(*c*) *Staining of the chromatin*

Out of a total of 49 central pronuclei, some fixed in Zenker's fluid, some in Perenyi's, and all stained with Heidenhain's iron-haematoxylin, 31 showed globules which were stained pink with eosin or were colourless or faintly stained in contrast to the deep purple or blue-black stain of the remainder of the chromatin. These differences might be due to several factors: differences in fixation, differences in staining technique, or differences arising from the actual structure or development of the pronuclei. Whatever the cause, wherever the pink, pale or colourless globules are present in a pronucleus, it must indicate some difference between those globules and the rest of the pronuclear particles. In the mouse pronuclei Lams and Doorme (1908) described a colourless plasmosome; in the pronuclei of the same animal Sobotta (1895) described the remains of the chromatin nucleoli which appeared as rings filled with karyolymph after the scattering of the chromatin over the other parts of the pronucleus. The exact nature of the pale, colourless or eosinophilic globules in the ferret has not been determined. To eliminate certain of the factors mentioned above as possibly responsible for the differences between the pronuclei in this respect, the Chi Square method was employed.

It was shown that there was no significant association between the fixative and the coloration of the chromatin particles ($\chi^2 = 1{\cdot}408$; $n = 1$; $P < 0{\cdot}20 > 0{\cdot}30$). Thus, neither the pronuclei fixed in Perenyi's fluid nor those fixed in Zenker's fluid showed such an excess of the pink, pale or colourless globules as could not

be accounted for by chance. The Chi Square test was also applied to prove whether there was any association of the colour of the pronuclear particles with the depth to which the section as a whole was stained with haematoxylin. There was no dependence of the one on the other ($\chi^2 = 0{\cdot}562$; $n = 1$; $P < 0{\cdot}50 > 0{\cdot}30$). Finally it was shown that the coloration of the particles was independent of the time after insemination ($\chi^2 = 1{\cdot}306$; $n = 1$; $P < 0{\cdot}30 > 0{\cdot}20$). So far, therefore, it has been impossible to demonstrate any cause of the pink, pale or colourless particles in the pronuclei. It is possible, however, that the time after insemination is not a sufficiently fine indication of the stages of development of the pronuclei; for out of 11 well-defined peripheral pronuclei in which the contents were granular or globular, not one showed any pink or pale or colourless particles, whereas out of 49 central pronuclei 31 showed such particles. Since the probability of the occurrence of a pronucleus with one or more of these particles is 31 : 49, and the probability of the occurrence of a pronucleus without such a particle is 18 : 49, then, on the assumption that the same factors are at work in the production of the staining reaction in both the central and peripheral pronuclei, it is possible to calculate the chances of all the particles being stained a deep purple or blue-black in the eleven peripheral pronuclei. Details of the theory and method will be found in Pearl (1923), pp. 236–7. In the present instance $p = \frac{31}{49}$; $q = \frac{18}{49}$. The last term of the expansion of the binomial expression $(p + q)^{11}$ gives the probability of the occurrence of 11 pronuclei all with purple particles. The value of this term is 0·000016, i.e. the odds are more than 50,000 to 1 against such an occurrence. Hence one may confidently assume that the factors responsible for the production of the eosinophilic or pale or colourless particles were not acting to anything like the same degree on the peripheral pronuclei.

It has already been shown that the large and medium-sized particles are characteristic of the pronuclei in the later stages after insemination, and therefore the Chi Square test was applied to prove whether there was any association between the size of the particles in the pronuclei and the presence or absence of the pink or pale particles. No such association was found ($\chi^2 = 1{\cdot}2$; $n = 1$; $P < 0{\cdot}30 > 0{\cdot}20$).

The conclusions to be drawn from these tests are as follows: eosinophilic, pale, or colourless particles are much more commonly found in central than in peripheral pronuclei. The occurrence of these in the central pronuclei is independent of the fixative, the depth of the basic stain and the time after insemination. It is not possible to show any association between the stage of development of the central pronuclei and the presence or absence of these particles.

(*d*) *Position of the chromatin particles*

Kremer (1924) described at a fairly late stage in the development of the pronuclei of the mouse an adhesion of chromatic material to the pronuclear membrane. In mouse ova and in those of the rat Kremer considered that an increase of the chromidial substance of the cytoplasm was connected with an

elimination of chromatin from the pronuclei, and suggested that the particles on the membrane might pass out from the pronuclei. Out of 97 of the ferret pronuclei under examination, 25 showed chromatin collected to a greater or less extent in the outer parts of the pronuclei (fig. 6); while in the rest the chromatin was central (4 pronuclei) or was scattered fairly uniformly (68 pronuclei). The Chi Square test showed that the position of the particles was independent of the time after insemination ($\chi^2 = 0{\cdot}96$; $n = 1$; $P < 0{\cdot}50 > 0{\cdot}30$). It was found that there was a highly significant association between the arrangement of the chromatin particles in the pronucleus and the presence of the eosinophilic or colourless particles ($\chi^2 = 8{\cdot}094$; $n = 1$; $P < 0{\cdot}01$). In the pronuclei, where the chromatin was peripheral, there was a much greater proportion showing only purple particles. The explanation of this is obscure, partly because there is no adequate measure of the time after fertilisation. There was no association between the position of the chromatin particles and the size of the particles predominating in the pronuclei ($\chi^2 = 0{\cdot}13$; $n = 1$; $P < 0{\cdot}80 > 0{\cdot}70$).

THE RETICULUM

A reticulum in the pronuclei of the ova of different Mammals has been described by various authors. Kremer (1924) has pointed out that during the very early stages of pronuclear development in the mouse there is no reticulum. Commonly it is not made clear in the literature whether the reticulum is an early or merely a later phenomenon. In the series of ferret specimens examined some of the pronuclei presented fine strands of reticulum, others a moderately coarse and some a very coarse reticulum (fig. 3). There were various differences also in the extent to which the different parts of the reticulum were continuous with each other. In some pronuclei there were long strands; in some the reticulum appeared merely as rows of granules (fig. 5). In a number of the pronuclei deeply stained chromatin particles formed varicosities on the reticulum (fig. 2). For the most part the medium-sized and larger chromatin particles showed no distinct relationship to the reticulum.

The formation of a reticulum can occur soon after the stage at which the pronuclei appear homogeneous. It was found in both male and female pronuclei when they were peripheral.

The reticulum was classified under the headings: Indefinite or Absent; Fragmentary or Granular; Fine; Medium; Coarse. These characteristics were studied in relationship to the position of the pronuclei—peripheral, sub-central or central. There was no significant association between the position of the pronuclei and the presence or condition of the reticulum ($\chi^2 = 0{\cdot}87$; $n = 2$; $P < 0{\cdot}70 > 0{\cdot}50$). The Chi Square method was also applied to test association between the condition of the reticulum and the number of hours after insemination. To avoid fallacies due to fixative and staining, only specimens fixed in Zenker and stained by Heidenhain's iron-haematoxylin were used. There was

found to be no association between the time and the reticulum ($\chi^2 = 1{\cdot}8$; $n = 1$; $P > 0{\cdot}10 < 0{\cdot}20$).

The Chi Square revealed at first an apparent association between the fixative and the reticulum. The data upon which the tests were made is shown in Table VI. In order to obtain sufficient numbers of instances in the various

Table VI. *Relationship of reticulum to fixatives and stains.*

(The numbers represent individual pronuclei.)

Fixative and staining	Reticulum indefinite or absent	Reticulum fragmentary or granular	Reticulum fine	Reticulum of medium thickness	Reticulum coarse	Totals
Zenker's fluid; Heidenhain's iron-haematoxylin	4	20	6	6	6	42
Zenker's fluid; Mayer's haemalum	4	2	10	0	0	16
Perenyi's fluid; Heidenhain's iron-haematoxylin	3	9	3	10	6	31
Mann's fluid; Heidenhain's iron-haematoxylin	1	0	0	0	0	1
Mann's fluid; Mayer's haemalum	6	0	0	0	0	6
Flemming's fluid; Heidenhain's iron-haematoxylin	4	2	0	0	0	6
Flemming's fluid; eosin tinted only	11	4	4	0	0	19
Totals	33	37	23	16	12	121

cells of the Chi Square, the groups of Table VI had to be merged into larger groups. Thus the fixatives were first classified as "Zenker" and "Non-Zenker," and the reticulum was classified according to its absence, granularity or presence as continuous strands, not broken up into granules. The results of the first test were: $\chi^2 = 10{\cdot}4$; $n = 2$; $P < 0{\cdot}01$. When, however, all the specimens fixed in Flemmings fluid were eliminated, and the test was carried out with the specimens fixed some in Zenker's, some in Perenyi's and some in Mann's fluids (including Mann's fluid with formol), there was found to be no significant association of reticulum and fixative ($\chi^2 = 3{\cdot}3$; $n = 2$; $P < 0{\cdot}20 > 0{\cdot}10$). The Flemming specimens contributed heavily to the groups containing absent or indefinite reticulum and granular reticulum. Since most of these Flemming specimens were merely tinted with eosin, and not otherwise stained, the reticulum was less likely to be demonstrated than in deeply stained specimens. It appeared therefore possible that if these eosin-tinted specimens alone were excluded, no association would be found between reticulum and fixative. The Chi Square test showed such to be the case ($\chi^2 = 5{\cdot}2$; $n = 2$; $P < 0{\cdot}10 > 0{\cdot}05$). The apparent high association between fixative and reticulum can therefore be sufficiently accounted for by the faint staining of the majority of the specimens that had been fixed in Flemming's fluid.

A comparison of the reticular conditions under Zenker fixation with those

under Perenyi fixation was made by the Chi Square method, only the central pronuclei stained with Heidenhain's iron-haematoxylin being chosen. There was no significant dependence of the reticular conditions on differences between those fixatives ($\chi^2 = 2{\cdot}7$; $n = 2$; $P < 0{\cdot}30 > 0{\cdot}20$). Even when the specimens fixed in Zenker's fluid and stained by Mayer's haemalum and eosin were included, the Chi Square test did not reveal any significant result due to this type of staining ($\chi^2 = 1{\cdot}4$; $n = 2$; $P < 0{\cdot}50 > 0{\cdot}30$). This last result also indicates that the specimens fixed in Mann's fluid did not produce any significant preponderance of pronuclei with reticula belonging to any of the classes shown in Table VI.

The influence of the different methods of staining was further investigated by the application of the Chi Square test to the Zenker-fixed specimens, some of which were stained with Heidenhain's iron-haematoxylin and others with Mayer's haemalum. The condition of the reticulum according to this direct test was independent of the staining method ($\chi^2 = 1{\cdot}8$; $n = 1$; $P < 0{\cdot}20 > 0{\cdot}10$). On the other hand, indirect evidence of the influence of staining was obtained in the following way. The pronuclei fixed in Zenker's fluid, Mann's fluid, and Perenyi's fluid were considered. When the pronuclei stained with Mayer's haemalum were all excluded, the result of the Chi Square test showed no association between fixative and reticulum ($\chi^2 = 2{\cdot}9$; $n = 2$; $P < 0{\cdot}30 > 0{\cdot}20$). When the pronuclei fixed in Mann's fluid and stained with Mayer's haemalum were alone excluded, and those fixed in Zenker's fluid and stained with Mayer's haemalum were still retained, there was still no significantly positive result ($\chi^2 = 1{\cdot}1$; $n = 2$; $P < 0{\cdot}70 > 0{\cdot}50$). When, however, the pronuclei fixed in Zenker's fluid and stained by Mayer's haemalum were excluded, and all those fixed in Mann's fluid were retained, there was a significantly positive result ($\chi^2 = 6{\cdot}5$; $n = 2$; $P < 0{\cdot}05 > 0{\cdot}02$). In brief, the position may be stated thus. When all the pronuclei fixed in Zenker's, Mann's or Perenyi's fluids are considered, irrespective of staining, there is no association between the reticulum and the fixative. When all the Mayer-stained pronuclei are excluded, or when only the Mann-fixed Mayer-stained pronuclei are excluded, the reticulum appears still to be independent of the fixative; but when only the Zenker-fixed Mayer-stained pronuclei are excluded, there is a distinct relationship between the fixative and the reticulum. Examination of Table VI reveals the fact that many of the Zenker-fixed Mayer-stained specimens had fine reticula. The positive Chi Square result indicates that this type of staining had a statistically appreciable tendency to produce finely granular reticula.

THE PRONUCLEAR MEMBRANE

(*a*) *Wrinkling of the membrane*

Before the first segmentation of the fertilised ovum, the pronuclear membrane must disappear. It is natural to suppose that, as described by Sobotta (1895) in the mouse, a preliminary to this disappearance is the wrinkling of

the membrane, noted in the present series of specimens in many instances. The Chi Square test showed that there was no significant association between the time after insemination and the degree to which the membrane was wrinkled —definitely, moderately or slightly—($\chi^2 = 2{\cdot}61$; $n = 1$; $P < 0{\cdot}20 > 0{\cdot}10$). The wrinkling of the membrane was also independent of the fixatives used ($\chi^2 = 2{\cdot}211$; $n = 2$; $P < 0{\cdot}50 > 0{\cdot}30$).

In some pronuclei the wrinkling of the membrane was general; in others it was most marked at the sides where the two pronuclei were adjacent (fig. 2). This difference in location was independent of the time after insemination ($\chi^2 = 2{\cdot}52$; $n = 1$; $P < 0{\cdot}20 > 0{\cdot}10$).

(*b*) *Completeness of the membrane*

To obtain evidence of the commencing disappearance of the pronuclear membrane and possible fusion of the pronuclei, notes were taken of the completeness or incompleteness in the various specimens. In determining the condition of the membrane all the specimens which were fixed in Flemming's fluid were excluded, since in these, most of which were tinted with eosin, the membrane was frequently indistinct. Out of 26 pairs of central pronuclei, seven pairs had membranes which were of doubtful completeness, and in one pair the membrane seemed clearly to be common to the two pronuclei. With one exception these eight pairs were from a ferret killed 64¼ hours after insemination. The remaining specimen, in which the completeness of the pronuclear membranes was doubtful, was from a ferret killed 76½ hours after insemination. In all the other specimens, taken from ferrets killed 41½, 47½, 51¾, 64¼ and 76½ hours after insemination, the membranes were complete. It was thought possible that where the two pronuclei overlapped in the section doubt might be thrown on the completeness of the membrane—a doubt simply due to difficulties of observation. The Chi Square test showed that the recorded completeness of the membrane was independent of the overlapping of the two pronuclei ($\chi^2 = 0{\cdot}72$; $n = 1$; $P < 0{\cdot}50 > 0{\cdot}30$).

So far, then, it has merely been demonstrated that the only specimens showing doubtful completeness of the pronuclear membrane were obtained comparatively late after insemination. There is very little evidence to indicate whether or not actual fusion of the pronuclei occurs, as it has been stated to do in the rabbit (van Beneden, 1875), or whether the two pronuclei remain separate up to the stage of the first segmentation, as is the general rule (Sobotta, 1895: mouse; Rubaschkin, 1905: guinea-pig; O. van der Stricht, 1923: various Mammals).

THE COMPARATIVE METHOD

Statistical treatment of the data has so far proved chiefly negative relationships between phenomena, and it may be asked whether it is necessary to confine oneself to such statements as can be proved statistically. The usual method with material such as is now being studied is to arrange the different

specimens in as reasonable an order as possible so as to indicate a series of steps from the state of peripheral pronuclei, completely basiphilic, to the spireme of the first segmentation spindle. It may be asked whether it is not possible to fit the specimens at present under consideration into the schemes described by other authors for other animals. Such a method should be used with caution. In the first place, the schemes so described are simply the interpretations placed by the authors upon the specimens studied. In the second place, minor differences are present in different animals, and it entails considerable assumptions to transfer information from a rodent's ovum, poorly supplied with lipoid, to the ferret's ovum, which is very richly supplied with lipoid.

One of the most thorough descriptions of early developmental stages was that of Sobotta (1895) on the mouse. In this animal the chromatin of the pronuclei was stated to be at an early stage in the form of large masses, one in the male pronucleus, several in the female. Then followed a subdivision of the chromatin and a spreading of it over the rest of the pronucleus as fine particles. These then condensed to form thread-like fragments, which later became a single much wound thread. Thus arose the spireme of the first segmentation spindle.

According to Kremer (1924) in the mouse pronucleus there is at a very early stage no typical reticulum. The chromatin granules, after being arranged around a single nucleolus and near the pronuclear membrane, unite to form large masses. Later still there is a separation of the chromatin substance and particles are laid down on the reticulum. Subsequently much of the chromatin disappears.

Both Sobotta and Kremer described pale globules, probably formed by a loss of basiphilic material, or of the staining quality of the chromatin.

Lams and Doorme (1908), also working on the mouse, described the fragmentation of the chromatin into small masses, arranged at the pronuclear membrane or along fine filaments which were placed radially about the large plasmosome. Later this plasmosome was found to disappear, the chromatin granules were noted to unite and form with the network rodlets—the chromosomes at the spireme stage of the first segmentation spindle.

In the rat Sobotta and Burckhard (1911) described for the early stages a fine linin framework with large chromatin nucleoli; for the later stages a more thread-like spreading of the chromatin on the framework.

To Kremer (1924) it appeared as if at a certain stage in the rat the smaller chromatin particles arose by a kind of budding from the chief nucleolus. This chromatin then spread out as finer or coarser divisions on the reticulum, and later much of it disappeared.

Huber (1915) gave little detail regarding the rat at this stage of development.

For the guinea-pig Lams and Doorme (1908) stated that a process occurred similar to that already described for the mouse.

Among Carnivores, to which class the ferret belongs, a fairly full description

of the very early development of the cat was given by R. van der Stricht (1911), but he did not give very much detail of the minute processes undergone by the pronuclei. He wrote of the nuclein granules, and masses occurring in the pronuclei as they increased in volume, and numerous chromatin globules in the pronuclei when large.

Longley (1911) and Hill and Tribe (1924) gave descriptions of a few specimens of pronuclear stages obtained from the cat.

O. van der Stricht (1923) gave information concerning the developing ova of the dog; but was more concerned with the cytoplasm than with pronuclear transformations.

With the aid of these data concerning other animals, an attempt may be made to arrange a possible sequence of phenomena in the pronuclei of the ferret.

At the outset several assumptions based on the results obtained in the preceding sections may be made. It may perhaps be assumed that in the early stages the chromatin particles tend to be smaller than in somewhat later stages, that the pronuclei in the early as well as in the later stages possess a reticulum, and that the presence of a globule with a non-basiphilic centre is a mark of an intermediate or late stage of development. An attempt may then be made to select a number of specimens illustrating a possible developmental process.

In three specimens (nos. 2, 75 and 77), all with central pronuclei, there were no large chromatin particles. Two of the specimens were fixed in Flemming's fluid and tinted with eosin, so that the basiphilic reaction of the chromatin was not shown. In all three the reticulum was granular. In no. 2 (fig. 5), a Zenker specimen stained with Heidenhain's iron-haematoxylin, the small globules of chromatin formed definite varicosities on the reticulum. Some of the chromatin was partly decolorised.

These three specimens may perhaps be taken to illustrate a stage occurring early after the stages of peripheral pronuclei described above. Three other ova may serve to illustrate a possible subsequent stage. In no. 69, a Flemming-fixed specimen tinted with eosin, the pronuclei showed granules of varying sizes, none very large, and a reticulum which appeared to be made up of rows of granules. Ova nos. 93 (fig. 1) and 99, fixed in Perenyi's and Zenker's fluids respectively, and both stained with Heidenhain's iron-haematoxylin, showed globules of moderate size. The reticulum was rather coarse and showed basiphilic granules. In one of the pronuclei in no. 99 there was one moderately large pale globule. Each of the pronuclei of no. 93 possessed a moderately large pale purple sphere with a dark purple membrane.

As possibly illustrating much later stages, five specimens with large chromatin masses in the pronuclei may be discussed. All the pronuclei were central and were stained with Heidenhain's iron-haematoxylin. In ovum no. 85 the pronuclear particles were stained a deep purple and the reticulum was formed of strands of granules and globules. In no. 46 all the particles were stained a deep purple; the reticulum was discontinuous, formed of strands and

rods. In ovum no. 86 a few of the large globules were light purple in contrast to the deep purple of the rest; the reticulum was moderately fine with varicosities. In no. 88 all the particles were a deep blue-black; the reticulum was coarse and similarly stained. In no. 89 there was a light purple mass in one pronucleus; the rest of the particles were deep purple; the small chromatin globules and granules were spread in strands. This description gives, it will be seen, no very coherent picture. If it be assumed that it represents a late stage of development, as contrasted with the peripheral pronuclei described above, and possibly with the central pronuclei described earlier in this section, then it may be supposed that intermediate stages will be represented by pronuclei containing granules of varying sizes, some large, some intermediate, some small. On the other hand, some of these last-mentioned specimens may represent a stage in which the chromatin is again divided after being aggregated into large masses. A review of these specimens showed that it was impossible to arrange them in any satisfactory scheme. In some of them the reticulum was fine, in others moderately fine, in others coarse. The chromatin particles in some were all stained a deep purple with Heidenhain's iron-haematoxylin; in others there were one or more pink or pale purple or colourless globules.

In the series of central pronuclei as a whole, the pink or pale purple or colourless globules were large or moderately large. In one specimen (no. 16) there was noted a reticulum with small swellings, mostly stained pink with eosin. It was further interesting to note that specimens fixed in Zenker's fluid and stained with Mayer's haemalum and eosin, presented pronuclei that were less deeply stained by the basic stain than were the nuclei of other tissues in the same section. This was not the case with specimens fixed in Zenker and stained by Heidenhain's iron-haematoxylin; nor was it the case with specimens fixed in Mann's fluid and stained with Mayer's haemalum.

The question raised by Kremer (1924) as to the elimination of chromatin and the production of chromidial substance in the cytoplasm, it is intended, shall be discussed in a subsequent communication. So far as investigations have proceeded at present, there appears to be no evidence of a diminution of chromatin from the pronuclei.

DIFFERENCES BETWEEN THE PRONUCLEI

The possibility of distinguishing the male from the female pronucleus is naturally one of very great interest. It is intended that size-differences, which are frequently claimed as a characteristic, should form part of the subject of a future communication. Differences in position, also, are more adequately treated in connection with the cytoplasm and polar bodies.

The most conclusive proof of the derivation of a pronucleus is the presence of a spermatozoon tail near it; but it should not be forgotten that a tail might follow the head of a spermatozoon into the ovum, and then be severed from the head or male pronucleus and come to lie nearer to the female than to the

male pronucleus. It would therefore be unsound to argue from the proximity of a sperm tail that either the male or the female pronucleus was the larger, or that they had certain differences of structure, unless these characteristics were found in several instances.

The occurrence of the sperm tail in the fertilised ovum was demonstrated by O. van der Stricht (1902) in ova of the bat. Sperm tails are also found in the ova of the mouse (Lams and Doorme, 1908), guinea-pig (Lams and Doorme, 1908), rat (Sobotta and Burckhard, 1911). O. van der Stricht (1923) stated that sperm tails were only exceptionally seen in the ova of the dog, and further pointed out that their occurrence had not been observed during the investigations conducted by R. van der Stricht (1911) on the ova of the cat.

In the present collection, out of 54 ferret ova at the pronuclear stage, apparently suitably fixed and stained, only one showed definitely the presence of a sperm tail within the ovum. In another specimen a structure which was very probably a sperm tail was observed. In the uterine tube sperm tails are observed seldom, relative to the frequency with which deeply stained sperm heads are seen. The failure to demonstrate tails inside the ovum is therefore at least as likely to be due to technique as to absence of the tails. It was to technical causes that O. van der Stricht (1923) attributed the apparent absence of tails from the ooplasm.

The ovum in which the definite sperm tail was observed was no. 88 (fig. 7). In this ovum the two pronuclei were centrally placed, in contact. One of them, B, was more truly central in the section than the other, A, for pronucleus A was placed a little more towards 9 o'clock. Both were spherical but flattened against each other. The membranes were moderately fine, darkly stained, somewhat wrinkled and possibly incomplete. The chromatin was in the form of deeply blue-black globules, large irregular lobulated masses and granules of various sizes. The reticulum was in parts coarse and deeply stained. Passing from pronucleus A towards 7.30 o'clock was a definite dark greyish stained fine strand actually in the ovum. This was separated by a small clear space from the pronucleus. The ratio of the volumes of the pronuclei calculated from the formula for the volume of an ellipsoid was roughly: A : B as 45 : 60. The pronucleus near which the sperm tail was found was therefore the smaller. No structural difference between the pronuclei was detected.

If the direction of the tail indicated the path of the sperm pronucleus, the latter must have entered near the present position of a polar body.

In ovum no. 97 the pronuclei were both peripheral, of approximately equal size and of similar structure, consisting of medium-sized and small globules and granules, all stained a deep purple, a reticulum and a fine unwrinkled membrane. Near pronucleus A on the surface of the ovum was a sperm tail. A fine thread-like structure in the ovum was possibly a continuation of the sperm tail to the pronucleus. Pronucleus B was nearer to the polar bodies.

The presence of a centrosome was used by Sobotta and Burckhard (1911) as an indication of the male pronucleus in the rat. These authors held that the

sperm-centrosome divided later to give the two centrosomes of the first segmentation stage—a view held also by Sobotta (1895) for the mouse. Summarising his own work and that of his colleagues, O. van der Stricht (1923) stated that sperm-centrosomes and sperm-asters and traces of ovular centrosomes were visible at certain stages of fertilisation in the ova of the bat, guinea-pig and dog.

Among the pronuclear specimens of the ferret at present under consideration, no aster or centrosome was detected.

Among structural differences that have been described between the two pronuclei is the presence of a greater number of chromatin particles in the female pronucleus of the mouse (Sobotta, 1895). This difference was not observed as a constant feature in the ova of the ferret, and even when there was an apparent difference in the quantity of chromatin it was impossible to state which pronucleus was male and which female.

Out of ten ova in which both pronuclei were peripheral, eight showed differences in structure to a greater or less degree. Reference may be made for details of some of these to the section, above, in which the structure of the early stages of the pronuclei is discussed. These differences, in some instances at least, appear to be concerned with the rate of development of the two pronuclei. Of greater interest is the difference which existed in some ova between the pronuclei when these were at the centre of the ovum. Out of 49 ova in which the two pronuclei were central, nine showed pronuclei which differed in structure or staining, apart from size, shape, position or the proximity of sperm tails. These differences varied considerably from ovum to ovum. Thus in one ovum (no. 5) the chromatin was more uniformly distributed in one pronucleus than in the other; in one (no. 14) the chromatin of one pronucleus was more indefinite and more pink stained, while the reticulum was more abundant; in a third (no. 85) there were larger globules of chromatin and probably actually more chromatin in one pronucleus than in the other. In ovum no. 93 (fig. 1) one pronucleus differed from the other by possessing a more continuous reticulum, a chromatin globule that was paler than the rest and a central area clear of chromatin. It may be reasonably suggested that such differences as were observed in the structure of the two pronuclei might be attributed to:

(1) Differences in rate of development, notable in the early stages, but less notable later, because in the long resting period, when the pronuclei are together in the centre of the ovum, there is time for them each to arrive at a similar condition preparatory to the formation of the first segmentation spindle.

(2) Temporary differences in the physico-chemical state of the pronuclei, of no great significance.

(3) Sexual differences.

To proceed further than a mere record of these varied differences and possible causes would obviously be to indulge in profitless speculation.

A TRINUCLEATED OVUM

R. van der Stricht (1911) described the arrangement of three pronuclei in a fertilised ovum of the cat. He interpreted this as due to the penetration of the ovum by two sperms. Hill and Tribe (1924) also gave instances of trinucleated ova from the cat, which they also presumed to have arisen by double fertilisation. Kremer (1924), mentioning a trinucleated ovum of the mouse, pointed out that such a condition might be due to the fertilisation of a binucleated mature ovum. In a recent investigation of the pluriovular follicle the author (1928) paid attention also to the plurinucleated ovum. The literature seems to indicate that binucleated ova are comparatively rare. In the ferret not one of the sections of 496 adult ovaries examined was found to contain such an ovum. On the other hand, it is known that polyspermy in other animals is not uncommon (Wilson, 1925, p. 416), and therefore it seems more reasonable to attribute a trinucleated fertilised ovum to this phenomenon than to the previous existence of a mature binucleated ovum.

In ovum no. 45 of the present collection there were three pronuclei. Two (A and B) were centrally placed, almost in contact. They possessed chromatin globules and granules of various sizes, fairly uniformly scattered through the pronuclei. One globule in each pronucleus had a colourless centre; the remainder were stained blue-black. The reticulum was moderately fine. There were no structural differences between these two pronuclei. The third pronucleus, C, was placed in a section subsequent to the lowest section containing the nearer of the other two pronuclei, so that it was not in contact with the others. It was situated about half-way between the centre of the section and 7 o'clock. It resembled the other two in structure, except that it contained no pale globule. The ratio of the volumes as calculated from the formula for the volume of an ellipsoid was: A : B : C as 1·13 : 1·14 : 1·00. Pronuclei A and B were therefore of similar volume; while pronucleus C was distinctly smaller.

ACKNOWLEDGMENTS

The ova used for the above investigations were obtained from the collection in the Department of Anatomy of Edinburgh University, some specimens being prepared by Prof. Arthur Robinson and some by the author during his tenure of a demonstratorship and research studentship in Edinburgh. The study was commenced in Edinburgh, but the greater part of it was carried out in the Medical College of the University of Manitoba. The author owes a great debt of gratitude to Prof. Robinson for his generosity in lending the specimens for examination in Winnipeg. A part of the expenses entailed in the preparation of the specimens was defrayed by the Moray Fund of Edinburgh University.

For invaluable assistance in the statistical work of the paper the author wishes to express his thanks to Dr C. H. Goulden of the Dominion Rust Research Laboratory, Winnipeg.

SUMMARY

The purpose of this investigation has been partly to obtain detailed information upon the earliest stages of development of the tubal ova of the ferret, and partly to demonstrate the type of results ensuing from statistical methods not hitherto applied in this way to such specimens.

Serial paraffin sections, 10 microns thick, of 101 ova of the ferret were examined, from 30 different ovaries and 19 different animals. Out of these ova, 71 were at the pronuclear stage of development, and in them the pronuclei were examined in detail.

Statistical treatment was applied to the data, and the statistical method chiefly employed—the Chi Square method—has been explained (p. 264).

Since the actual number of hours that elapsed after fertilisation cannot be determined, a measure of the progress of development is obtained from the position of the pronuclei at the different stages of their migration towards the centre of the ovum. With the aid of this it has been proved that in this collection of specimens, treated as a whole, the number of hours that elapsed between the insemination and the death of the animal afford a measure of the progress of development of the ovum (p. 265). The position of the pronuclei, arranged according to the number of hours after insemination, is given in Table I (p. 266).

Allowance having been made for the possible dominating influence of abnormal specimens in so small a collection of peripheral pronuclei, the probable early transformations of the pronuclei are indicated (p. 267).

There was a highly significant association between the size of the chromatin particles in the pronucleus and the time after insemination (larger and medium-sized particles being found in the later stages). This association existed only in specimens fixed in Perenyi's fluid. Owing to the smallness of the numbers of the specimens it was impossible to prove that this association between time and the size of the particles really indicated an association with the development of the ovum or pronucleus. There was a highly significant association between the size of the particle and the fixative, Perenyi's fluid tending to give larger particles. There was, however, no significant association between the time after insemination and the fixative, and therefore the association between the time after insemination and the size of the particles could not be accounted for by the fixation.

Eosinophilic, pale or colourless particles were found in 31 out of 49 central pronuclei. No possible cause of these could be demonstrated. They occurred independently of the fixative and independently of the depth to which the rest of the section was stained with haematoxylin, and independently also of the time that had elapsed between insemination and death. It was shown (p. 271) by the theory of probability that the factors responsible for the production of these particles were not acting to anything like the same extent on the peripheral pronuclei as on the central.

The position of the chromatin particles—peripheral, uniformly scattered

or central—in the pronuclei was independent of the time after insemination and also of the size of the particles predominating in the pronuclei. Among the pronuclei where the chromatin was peripheral there was a much greater proportion showing only purple particles.

A reticulum occurred in pronuclei fixed either early or later in their development. Different varieties of reticulum were found—fragmentary or granular, fine, medium, and coarse. The presence or condition of the reticulum was independent of the position of the pronuclei, and of the number of hours after insemination. There was no association between the fixative and the condition of the reticulum; but specimens fixed in Zenker's fluid and stained with Mayer's haemalum and eosin produced a definite preponderance of pronuclei containing a fine reticulum.

There was no indication that the wrinkling of the pronuclear membrane was a preliminary to its disappearance. The wrinkling itself and the location of the wrinkling on the membrane were independent of the time after insemination. This wrinkling was also independent of the fixative used.

The only specimens showing doubtful completeness of the membrane were obtained comparatively late after insemination. There is very little evidence to indicate whether or not actual fusion of the pronuclei occurs.

An attempt is made (pp. 276–9) to indicate the possible developmental processes in the pronuclei with the help of information obtained from the researches of other authors on other Mammals. Few results are obtained from this substitution of the older and commoner method for the newer and less common statistical one.

A description is given of two specimens (p. 280) in one of which a definite spermatozoon tail was found in the ovum; while in the other a probable tail was observed. It is probably to technical factors (fixation and staining) that one must attribute the scarcity of such specimens.

No centrosome or aster was seen in any of the pronuclear ova.

Various inconstant differences in structure between the pronuclei are described (pp. 279–81).

A trinucleated ovum is described (p. 282). The condition is attributed to double fertilisation.

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WINNIPEG,
18th July, 1929.

Fig. 1

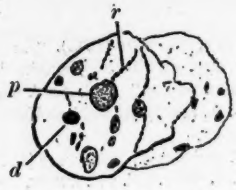

Fig. 2

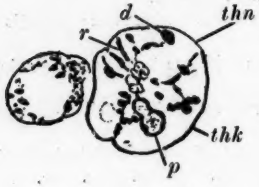

Fig. 3

Fig. 4

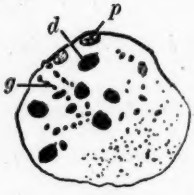

Fig. 5

Fig. 6

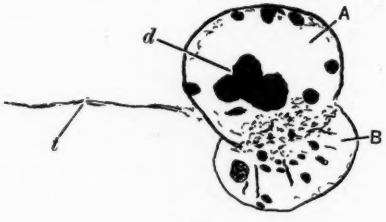

Fig. 7

EXPLANATION OF FIGURES

All the figures are pronuclei of the ferret, drawn with the aid of a camera lucida and are at a magnification of 1050 diameters.

Fig. 1. Ovum no. 93. Both pronuclei. Fixed in Perenyi's fluid; stained with Heidenhain's iron-haematoxylin. The reticulum is rather coarse, and shows basiphilic globules. (See pp. 278–81.)
int. Globule intermediate in staining between the dark and the pale globules.
m. Medium-sized globule of chromatin, darkly stained.
p. Pale purple sphere with dark purple periphery.

Fig. 2. Ovum no. 4. Both pronuclei. Fixed in Zenker's fluid; stained with Heidenhain's iron-haematoxylin and eosin. The pronucleus to the right is at a lower level in the section and is less sharply outlined. Deeply stained chromatin particles form varicosities on the reticulum. The membrane of the pronucleus on the left is most wrinkled at the side adjacent to the other pronucleus. (See pp. 273–6.)
d. A darkly stained globule of chromatin.
p. Pale globule of chromatin.
r. Reticulum with varicosities.

Fig. 3. Ovum no. 14. Both pronuclei. Fixed in Perenyi's fluid; stained with Heidenhain's iron-haematoxylin and eosin. The reticulum in the one to the right is very coarse. (See p. 273.)
d. Darkly stained globule.
p. Pale double globule.
r. Reticulum.
thk. Thick part of membrane.
thn. Thin part of membrane.

Fig. 4. Ovum no. 7. The two pronuclei, both peripheral. Fixed in Zenker's fluid; stained with Heidenhain's iron-haematoxylin and eosin. (See p. 268.)
e. Edge of ovum.
i. Inner pronucleus, larger, a ring with a pale centre and faintly purple lobulated periphery.
o. Outer pronucleus, smaller, a spherical homogeneous purple body.

Fig. 5. Ovum no. 2. One of the pronuclei. Fixed in Zenker's fluid, stained with Heidenhain's iron-haematoxylin and eosin. The reticulum appears merely as rows of granules. (See pp. 273–8.)
d. Darkly stained globule of chromatin.
g. Granules arranged in a row, indicating a reticulum.
p. Pale globule.

Fig. 6. Ovum no. 15. One of the pronuclei. Fixed in Perenyi's fluid; stained with Heidenhain's iron-haematoxylin and eosin. Both the pronuclei in this ovum had chromatin in globular form; but while one was central in the ovum, the other was peripherally placed. The chromatin is chiefly located in the outer parts of the pronucleus. (See pp. 268–73.)
l. Moderately large globule of chromatin.
r. Faint reticulum.
s. Small globule of chromatin.

Fig. 7. Ovum no. 88. Both pronuclei. Fixed in Zenker's fluid; stained with Heidenhain's iron-haematoxylin. Both the pronuclei were central in the ovum. One (A) is seen more nearly at its centre; the other (B) is seen nearer to one of its ends. (See p. 280.)
d. Darkly stained trilobar mass of chromatin.
t. Tail of spermatozoon.

MOVEMENTS OF THE NORMAL SHOULDER JOINT AND OF A CASE WITH TRAPEZIUS PARALYSIS STUDIED BY RADIOGRAM AND EXPERIMENT IN THE LIVING

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Almost eighty years ago, Duchenne, the tenacious and industrious, found that the mysteries of muscles were as surely revealed with "électrisation" upon the living as with scalpel upon the dead (1). Piecing together the puzzle of the dead, the normal, the paralysed and the stimulated muscles, he tackled functional anatomy with an intensive enthusiasm, not exactly a prominent feature in the text of to-day. This article, a chronological confession of changed opinion, is an insistence of the graphic power of radiology in the task of raising anatomy from the dead.

If a preparation of the humerus and scapula, from which everything has been dissected except the capsule of the shoulder joint, is held in the normal hanging position, it is impossible, with the scapula fixed, to abduct the humerus beyond the horizontal, but, with this relative position maintained, a very little forward and upward movement of the scapula now causes the glenoid cavity to carry the humerus into the vertical position.

Such demonstrations are responsible for the misconception common to many text-books that abduction of the arm is solely executed through the shoulder joint by the deltoid muscle, etc., to the horizontal, and that subsequent movement to the vertical is secured by the trapezius and serratus magnus muscles, etc., through the scapulo-thoracic articulation alone. While the various texts describe minor differences in detail, the above is the general impression conveyed regarding the main movements.

Many surgeons and teachers tell this story glibly and it appears with illustration in a recent radiographic atlas (2). I admit telling the story earnestly myself, showing the specimen one moment and causing students to inspect and palpate the living mechanism upon each other the next, with resultant discrepancies, but the main movements were apparently in accordance with traditional teaching.

The synchronised grace revealed by the ultra-rapid camera belies the idea of such definite staccato mechanism. Careful inspection and palpation of the living subject show that in raising the arm from the dependent to the vertical position, there is continuous movement not only at the shoulder joint, but also at the acromio-clavicular, the scapulo-thoracic and the sterno-clavicular

articulations, from the very beginning to the very end of the action. It is to be noted that the term "movement" does not imply direction.

To teach the varying position of the bones and the synergic muscular activity, recourse to radiogram is an essential addition to the methods of Duchenne.

As radiographic illustration of the shoulder joint with vertical elevation of the humerus is not shown in the texts known to me, has not been observed by the anatomists and clinicians I have questioned, and is an unusual procedure with striking results, figs. 1, 2, 3 (Plate I) are presented to compare the dependent, horizontal and vertical positions of an arm, which, as far as can be ascertained, has undergone no trials save exercise.

It is usually stated that no further humero-glenoid movement takes place beyond the horizontal plane indicated in Plate I, fig. 2, but in Plate I, fig. 3, there has been sufficient subsequent humeral movement from the second position to allow twice as much humeral articular surface to escape from the lower border of the glenoid cavity. It may not be inferred that there is therefore twice as much humero-glenoid or deltoid movement after the horizontal as before it, because, in the dependent limb, the lower border of the anatomical neck of the humerus is not necessarily on a level with the lower border of the glenoid cavity. It may rest one-third of the way up the glenoid cavity (4, 5). But there can be no doubt about the figures showing in decided manner the existence of a considerable degree of shoulder-joint movement from the horizontal to the vertical, between which probably one-half of the possible humero-glenoid movement from the hanging to the vertical positions of the arm is executed, and the deltoid is still in action.

In view of the fact that the relative position of the structures varies with the standing, prone and supine postures, because of the differing support or suspension of the limb, it is important to note that the illustrations have been made with the subject standing erect, in spite of the attendant loss of the steadiness desired by the radiologist. With this posture, the apparatus and orientation required the arm to be abducted in the coronal plane of the trunk. Now, the opinion (3) is held that a distinction must be made between this movement and that of advanced abduction where the humerus moves in the plane of the body of the scapula, said to be a much less complicated movement. Beevor (see p. 293, footnote 1) said the same description equally applied. However, it was decided to examine the problem, although of course the terminal position of the structures in the vertically upright arm is of necessity the same, irrespective of the plane traversed. If various persons are examined repeatedly, abducting the arm in the coronal plane of the trunk, in the plane at right angles to this, that is, advanced abduction, and in the intermediate planes, I find that corresponding levels of the arm in the various planes apparently give practically the same position of the scapula, but there is the following difference. With the arm in coronal abduction, the vertebral border is more closely applied to the chest wall while, in advanced abduction, this

border wings, except at its inferior angle, that is, in moving from the coronal to the advanced abduction plane the scapula pivots vertically upon its inferior angle, the medial angle moving posteriorly and the lateral one anteriorly. The easiest way to appreciate this difference is to swing the abducted arm horizontally to and fro. (If this is done passively, the winging becomes greater.)

Clinical estimation (6) of the shoulder-joint movement is made by the surgeon pressing down upon the point of the shoulder to fix the scapula while the patient tries to abduct his arm. The method, it is said, scarcely permits abduction to the horizontal, but I find it needs heavy pressure upon the shoulder point to prevent the scapula moving just a little and, provided the scapula is absolutely fixed so that a third person cannot feel it moving, I question whether the subject can even reach half-way to the horizontal. However, moderate downward pressure upon the shoulder point will prevent elevation of the arm beyond the horizontal, but the scapula moves a little. Still, it is an admirable teaching demonstration for the anatomy class to see a companion so simply incapacitated, and one well calculated to awaken the mind of the student to the possibilities of experiment upon the engines of the human body. But the opinion is held that this method causes the deltoid muscle and the shoulder joint to exhaust their possible sphere of movement. To determine whether this exhaustion is actually allowed to occur, it was decided to obtain a radiogram of the shoulder joint, the arm abducted as far as possible with the scapula previously fixed in position. The difficulty was met by tightly strapping a band over the point of the shoulder, and under the ischial tuberosity to take the place of the downward pressure of the surgeon's hands. Though it is difficult to prevent the scapula moving just a little, yet the arm can scarcely be raised to the horizontal, and fig. 4 (Plate I), obtained in this way, compared with figs. 2 and 3 (Plate I), shows that exhaustion of the shoulder-joint movement and of the deltoid muscle is not secured by this test. Just as Beevor inferred that serratus would not step into the breach left by trapezius paralysis, one might consider in this experiment that deltoid, having contributed its first instalment, refuses to complete the transaction until trapezius and serratus play their part. Probably it would be a more accurate explanation to maintain that deltoid is unable to complete its action because trapezius and serratus are prevented from securing the changes in apposition of the humero-glenoid and acromio-clavicular surfaces necessary to the further action of the deltoid muscle (cf. (19) p. 292). I am the more inclined to this statement from the fact that with one experimenter depressing the shoulder point, after the subject has abducted his arm as far as possible, a second examiner can quite easily raise the arm, but the scapula and clavicle also undergo their normal movement and force up the resistance. Now, if the defect were purely muscular, as has been suggested, one would expect the arm to be raised a certain extent with the scapula stationary. This manipulation may cause the patient a little discomfort in the shoulder joint.

In making the experiment seen in fig. 4 (Plate I), it is advisable to strap

down the points of both shoulders so as to prevent bending of the vertebral column to one side, with the production of results liable to misinterpretation.

I have devised another experiment to show the action of the shoulder joint and the deltoid muscle between the upright and horizontal positions of the arm. After the arm has been held erect, the experimenter endeavours to fix the scapula in position with his hands, while the patient is instructed to lower his arm. Resistance is experienced by the arm about 20 degrees before the horizontal plane at which the impediment becomes definite. It is, however, by no means an easy task to keep the scapula fixed in the position it occupies with the arm erect, and the employment of a well-developed experimenter and a moderately developed subject is suggested.

Again, the movement of the scapula may be demonstrated by causing the patient to elevate the arm to the horizontal when the experimenter fixes the humerus and the patient relaxes his muscles, whereupon the scapula can be pushed back, not into, but appreciably towards its resting position.

The clinician, desiring a ready guide in estimation of the fully abducted shoulder joint, will observe that in fig. 3 (Plate I) the shaft of the humerus is practically in line with the spine of the scapula, and this may be taken as some indication, provided he allows for individual variation, in which connection it is interesting to note Steinhausen's (7) radiographic investigation in 1899, to determine, in different individuals, the angular movement executed by the arms (not by the shoulder joint) from the side to the upright position: 2 per cent. showed 155 degrees, 29 per cent. 175 degrees, 26 per cent. 180 degrees, and a very few 195 degrees (8).

Examination of figs. 2 and 3, and even 4 (Plate I), with the scapula fixed, shows that abduction is not limited by contact of the great tuberosity with the acromion (9), nor yet by the tuberosity meeting the glenoid labrum (9). (The clinical experience that fractures of the tuberosity should be treated in horizontal abduction in order to keep the pathway of abduction clear, is not against the radiographic evidence, because all fractures not so treated are not subject to restricted abduction.) The general opinion (10), however, is that abduction is limited by tightening of the inferior part of the capsule (cf. (11)), but I prefer to consider that the movement is also controlled by neuro-muscular co-ordination, otherwise dislocation would not so readily ensue from unguarded movements, nor luxation from defective musculature (12, 13, 14, 15).

While we are dealing with the capsule it is opportune to review such statements as: "The looseness of the capsule is so great that the arm will fall about 2·5 cm. from the scapula when the muscles are dissected from the capsule, and an opening made in it to counteract the atmospheric pressure (16)." If a freshly dissected specimen with the capsule intact is held in the normal hanging position, the upper part of the capsule is quite taut and is responsible for the fact already noted that the lower margin of the anatomical neck of the humerus rests about one-third of the way up the glenoid cavity. If the capsule is opened, there will be no alteration in the position of the bones and they cannot be

separated, even by force, but on abducting the humerus the head will rotate downward and the upper part of the capsule become slack enough to allow separation of the bones.

Other features concerned with the arguments outlined above are more readily discussed in the following controversial review of the literature which will lead up to the case of trapezius paralysis.

In 1732 Winslow had found this region complicated enough to warrant his declaring that a treatise might be written on the numerous phenomena to be observed in the movement of the shoulder by the action of serratus itself(17). This is no idle statement.

Duchenne (1855), like Winslow, insisted on muscular synergism (a term Hunter used in 1777(18)), and gave detailed descriptions of the action of serratus, trapezius and deltoid, etc. He certainly appreciated the fact that serratus and trapezius come into action whenever the deltoid commences abduction, although, in his statement(19) "when the serratus is paralysed the patient can scarcely reach the horizontal plane and one might consider the deltoid defective were it not that when the scapula is thrust forward, he can erect his arm quite readily," it may be uncertain to credit him with suggesting a deal of humero-glenoid movement beyond the horizontal.

Cathcart(20) hit the nail on the head in 1882, declaring that the humerus moved on the scapula from the hanging position to the horizontal and also to the vertical above, but he decided that the chief movement occurred in the first phase, whereas radiograms show that the second is as active as the first. Cathcart also maintained that the scapula rotated throughout, with the exception of a short space at the beginning and at the end, but in no case have I ever found the scapula motionless to begin with. In some people the inferior angle of the scapula glides smoothly lateralwards the very instant the arm begins to be abducted, while in others the inferior angle actually moves slightly towards the middle line before the lateral movement occurs. In well-developed subjects showing this feature, sometimes the initial medial movement tends to disappear with repeatedly raising and lowering the arm in the process of examination, whereupon the inferior angle begins to glide lateralwards at the outset.

Cleland(21), in courteous agreement with Cathcart's criticism, added painstaking detail, and emphasised the variation of movements in different subjects. Only in one case did he find the slight medial movement of the inferior angle described above, but it does not appear to be so markedly exceptional; I find that it more often moves medially than laterally at the outset. Cleland also insisted upon the clavicle moving from the very commencement, not necessarily by elevation of its acromial extremity but by rotation, and he regarded individual variations in the behaviour of the outer end of the clavicle as due to the relative proportions of antagonistic forces. It is interesting to note his opinion, formulated before the adoption of radiographic methods, that the possible movements of joints and the relative distances of the attachments of

their muscles in the different positions of the joints cannot be studied except on the dead body.

In 1903, Beevor(22), again, insisted on alive anatomy with the plaintive yet warning statement: "I trust the time will come when the action of muscles will be taught on the living subject, together with the part which they take in the performance of simple movements." A disciple of the Hughlings Jackson teaching that the brain knows nothing of muscles but movements only, he added certain delicate pieces to Duchenne's picture-puzzles, declaring that serratus will not pull upon the scapula until trapezius first performs its allotted task, an explanation of the slight winging(23) of the scapula evident in the resting shoulder in trapezius paralysis, where serratus will not stand security for the absent trapezius and refuses to rotate the scapula until the deltoid has abducted the arm to an angle of 45 degrees from the side(24). It is questionable whether this action in paralysed conditions may be rightly described as the normal function of serratus, and in the case of trapezius paralysis to which subsequent reference is to be made both the normal and affected scapulae underwent immediate movement on the arms leaving the side. However, Beevor goes on to state: "Normally in advancing[1] the arm the scapula does not move until the humerus makes an angle of about 45 degrees, and then the inferior angle begins to move outwards by the commencing action of serratus, and when the humerus is horizontal the angle with the scapula remains constant, and the elevation of the humerus to the vertical position is completed by serratus." The second part of this quotation is the fallacy of accepted teaching. The first part, however, that the humerus must be abducted 45 degrees from the side, before the scapula moves and the serratus contracts, agrees with Cathcart's observation that the scapula does not move for a short space at the outset, until the angle is one of 30 degrees, when the contraction of serratus is difficult to appreciate. (The angular difference is not essential. Jones and Lovett(25) maintain that scapular mobility is so marked and variable that the character of all angular measurements in the shoulder region must necessarily be approximate.) But there is no doubt, according to Cleland and also the present investigation, that the scapula's inferior angle in certain people moves immediately lateralwards, and even where it makes a slight initial movement towards the vertebral column the muscles must in some measure be concerned. The point is that it is not stationary and therefore serratus and trapezius are not inactive. It should be noted here that the scapula's inferior angle, as a rule, not only moves medially before going laterally at the outset of arm elevation, but also repeats this overlapping at the end of lowering the arm before gaining the resting position.

The fact that normally the scapula undergoes movement from the outset of arm elevation may be considered at variance with Beevor's clinical statement: "Inability to abduct the arm without the inferior angle of the scapula moving outwards at once is a sign that either the deltoid is paralysed or that

[1] "The same description applies equally well to abducting the humerus"(24).

it is not acting owing to painful rheumatic changes in the joint, or because of ankylosis of the joint," but the scapular movement in these conditions is abrupt and clumsy, in contrast with the delicately accelerated gliding motion of the normal action.

However, the points which we have just been discussing are but side issues to the main contention that humero-glenoid movement is as active in the second phase of arm elevation as in the first.

Most text-books (26, 27, 28, 29, 30) have adhered to the traditional teaching, but some (27, 31, 32) having given such a preliminary statement then detail Cathcart's opinions, a context possibly of remark rather than belief, as the subsequent discussion of muscular action follows the usual description (33, 34). In Testut (35, 36, 37), however, Cathcart's teaching is emphasised, the researches of Duchenne (36) upon scapular movement and muscles are admirably presented and the subsequent description of the deltoid (37) action is in agreement.

In his recent book (38), 1928, *The Matrix of the Mind*, Wood Jones adopts the usual teaching of the deltoid acting to the horizontal, beyond which the angle between humerus and scapula remains constant, while serratus and trapezius rotate the scapula to secure vertical elevation of the arm.

This misconception has already been harped upon in detail, but Wood Jones raises other points directly bearing upon the question. For example, he explains why, at the commencement of arm elevation, the inferior angle of the scapula first moves medially, pauses, and then swings laterally, by stating that the pause marks the call upon the synergic action of trapezius to prevent the undesired medial movement (Plate I, fig. 5). Under such an assumption, what is to be the explanation, at the end of lowering the arm, for the occurrence of this same overlapping pendulum-like movement (cf. p. 293) at a time when the trapezius is actively concerned in the graduated lowering of the arm to rest? Would it not be simpler to suggest that Nature, with wonted economy, does not immediately goad trapezius into action when deltoid alone, at first, raises the arm efficiently in spite of a negative swing by the scapula's inferior angle, caused by the weight of the rising arm, and that as the task increases more muscles are harnessed to the work? Similarly, in lowering the arm trapezius is unyoked earlier with the corresponding mechanical inward swing of the scapula. It has, however, already been observed (cf. p. 292) that this medial movement may disappear with repetition of the exercise, as if the muscle were taught to anticipate the action. This movement of the inferior angle is very slight, and but momentary, and the above remarks are not to confuse the practical point that serratus and trapezius act at the outset of abduction.

Before broaching the subject of trapezius paralysis, it is necessary to be decided upon the facts of the normal action of trapezius and serratus. Although we have decided already that these muscles must be active the moment the inferior angle of the scapula moves, their action is better demonstrated by the following more vigorous methods. A well-developed subject is instructed to

abduct the arm while the examiner places one hand firmly upon trapezius and resists the patient's arm with the other. At a definite signal the subject reverses the action to adduction with the examiner again resisting. The alternate firming and softening of the muscle is quite definite in all planes of abduction and levels of the arm from the side to vertically upright. The serratus is readily examined in the same way with the same results. The activity of these muscles is even more strongly exhibited by palpating them while the patient, prone upon the floor, performs the exercise of raising and lowering the trunk, pressing his hands upon the floor. In this exercise, of course, the muscles are continuously in action, both during raising the trunk and lowering it against gravity.

It should again be pondered here whether the action of a muscle, with a paralysed companion, will be its normal action, and whether the deficient movement resulting from a paralysed muscle will be a true analysis of its action as a component in a movement.

To come to the subject of trapezius paralysis, the case in question was referred to me by the Director of Physical Culture, University of Aberdeen, prior to a course of remedial exercise, and two more cases have been examined.

The girl, almost 19 years of age, muscular and eager for athletics, complained of deformity of her left shoulder. The case is a good example of left trapezius paralysis, and examination revealed a tell-tale scar in the mid-sterno mastoid region received at operation when she was 2 years old.

On the affected side, with the subject standing erect, the scapula is $1\frac{1}{2}$ inches higher than its neighbour as regards the medial and inferior angles; the medial angle is 4 inches from the middle line instead of 2 inches and the inferior angle $3\frac{1}{2}$ inches instead of $2\frac{1}{2}$ inches. Accordingly, with the arm at rest, the medial border of the scapula slopes from below upwards and lateralwards, and there is slight winging of the bone. The point of the left shoulder and the acromial end of the clavicle droop and project, so that the front of the chest shows a deep transverse hollow. Plate I, fig. 6, shows the patient's back. In Plate II, fig. 1, the scapulae have been outlined upon the skin, but it will be seen that this surface-marking is approximate because of the movement occurring before the marking and photographing can be made. Plate II, fig. 2, gives a general view of the thoracic skeleton and both shoulders as far as possible upon a 15-inch plate, with the subject erect. These figures show the divergent position of both scapulae at rest, particularly the high tilt of the medial angle of the left one, the strain thrown upon the left sterno-clavicular articulation by the absence of trapezius and the adaptations of the thoracic skeleton.

It is immediately evident from these plates that it is more accurate to describe the affected scapula as higher than its companion, but it is usually stated that in trapezius paralysis the scapula drops to a lower level (39), although the descriptions of Duchenne (40) are meticulous to a degree. Certainly the shoulder joint and the scapula's lateral angle are lower, but the bone, as a whole, is higher in trapezius paralysis. By taking two X-ray plates together, both shoulders are shown as in Plate II, figs. 3, 4. In Plate II, figs. 2, 3, the

patient is standing but in fig. 4 supine, and the part played by the weight of the limb and the pitfalls attending the investigation are at once apparent. Not only, with careful orientation, does the lateral angle also become higher in this supine position but the bone sags postero-medially round the chest wall. A radiogram taken in the prone position more closely resembles one taken in the erect posture. Radiologists prefer to take plates with the subject recumbent, and steady, but in view of these facts it is hardly fitting for the clinician to examine an erect patient on the one hand with a "recumbent" radiogram on the other. Taking the above five figures of trapezius paralysis with the arms dependent in review, let us examine the reasons for the high tilt of the medial angle. The scapula is really a wonderful bone, probably best described as three plates meeting in the line of the spine, which must afford a powerful lever to the trapezius in dealing with the weight of the limb. In paralysis not only is there a loss of the suspensory action of the upper fibres upon the lateral parts of the clavicle and spine, but there is also a loss of the downward traction of the lower fibres upon the spine's medial part, both complementary actions, and, in addition, there is the serious fact that the levator scapulae and rhomboids are deprived of an antagonist. These facts and the weight of the limb would seem to account for the scapula's position. In a case of 17 years' duration it might be considered that these last three muscles would have undergone shortening, but although the medial angle is higher it is also more lateral, and while these muscles are now moulded in a new disposition their actual length may not be greatly altered. The case of serratus is rather different. Not only is the disposition of the muscle altered, but its upper fibres are shortened, and even if the lower fibres are not shortened their new alignment sets them to act at a disadvantage. Instead of regarding serratus as not stepping into the breach left by trapezius paralysis, it seems kinder to consider its sorry plight in the defection of its companion.

When the girl raises her arms, the immediate medial movement of the inferior angles of both scapulae, to my observation, is the same. There is no more medial swing of the affected scapula than of the sound one, but Wood Jones (38), in citing trapezius paralysis, states that when the deltoid acts, the scapula swings medially because of the lack of the synergising action of trapezius. To my mind, the discrepancy is present at rest, before movement begins at all, in the divergent position of both scapulae. To continue with Wood Jones' further discussion of trapezius paralysis: "The deltoid can still move the humerus until it is at a right angle to the scapula, but, owing to the rotation of the scapula it is unable to raise it to a right angle from the side of the body. The serratus magnus begins to contract when the deltoid has done its utmost and swinging the scapula outwards, raises the arm to the level of the shoulder, by restoring the scapula to its normal position." He continues that serratus will not play the synergising rôle of trapezius for deltoid, because in the ordered play of the components of the movement of raising the arm the serratus acts after the deltoid has done its utmost. These remarks are fraught with the usual

erroneous ideas of the normal action, but it is upon the movements in trapezius paralysis that attention is now directed. It has just been pointed out that in this case both inferior angles move together. In elevation of the arms to the horizontal the affected scapula is as active as its companion, but immediately before the horizontal plane is reached there is a remarkable occurrence. Suddenly, with the arm horizontal, the affected scapula describes an ungainly jerk downwards. From occupying a hunched position upon the shoulder, it suddenly drops, just as if it had disappeared through a trap-door, and, what is most striking, the arm still remains in the horizontal plane. The sudden scapular movement does not yield a proportionate elevation of the humerus, and it appears to be a gravitation caused by the weight of the arm, with little or no muscular control. This phenomenon is most marked when the arm is abducted in the transverse plane of the chest, and is not so evident and embarrassing if the arm is moved anteriorly during abduction. Plate II, figs. 5, 6, and Plate III, fig. 1, show the scapula before it has dropped, while the arm is still horizontal, and Plate III, fig. 2, is a radiogram of the position of the bones; again, Plate III, figs. 3, 4, show the surface and radiographic appearances after the scapula has dropped, and while the arm is still horizontal. It is not exactly easy to secure radiograms of the two "different horizontal positions." The phase is a matter of touch and go and cannot be controlled by the subject. The difficulties or plight of serratus in the dependent position of the limb have already been shown, but in Plate II, figs. 5, 6, and Plate III, figs. 1, 2, it is seen that these difficulties are aggravated by the weight of the rising limb. This causes the medial angle to ascend still further, and I consider that the ungainly jerk of the scapula may be explained as follows. Up to this point serratus is working hard, without adequate return, to get the glenoid cavity under the humeral head, and the moment this critical corner is reached, the pent-up energy of the muscle is released, as by a mechanical trigger, so that the scapula makes a sudden abrupt rotation upon the chest wall and under the humeral head. This is evident in the two radiograms comparing the "different horizontal positions." In the second the glenoid cavity is further round the chest wall, well under the humeral head, and there is less of the humeral head projecting than in the first. Now the scapula is making up for lost time in this jerk and accordingly there is no corresponding movement of the humerus. From the radiograms it might be considered that the movement is an ordinary rotation of the scapula, but examination of the living subject in action fully justifies the terms "jerk" and "drop." Serratus is not so embarrassed in advanced abduction because the slight winging of the scapula already described as normally occurring in this plane facilitates the action alignment of the muscle.

In Plate II, figs. 5, 6, it might be considered that deltoid is not working to advantage, but Plate III, fig. 1, of the anterior aspect, shows this is more apparent than real. Plate III, figs. 5, 6, show the appearances in vertical elevation and emphasise the low position of the affected shoulder in this

attitude. Except by bending the vertebral column, the patient can hardly reach the erect position which is unsteady and fatiguing. Radiograms, Plate III, fig. 7, of this position are easily mistaken, because although the humerus is not vertical the scapula swings so far round upon the chest wall that the body of the bone lies at right angles to the plate and in line with the shaft of the humerus, causing the radiogram to straighten out the angle artificially. Other orientations cause too many superimposed shadows for a satisfactory result.

Apart from the deformity and the annoying jerk of the scapula at the horizontal level of the arm, the girl experiences no disability in physical exercises save a certain anxiety of insecurity in hanging by the affected arm alone, and the inability, when in the prone position, with arms extended in front of the head, to raise this arm from the floor.

The problem in this case is the question of remedial exercises for aesthetic appearance. Development of serratus, and of latissimus dorsi with its scapular slip is readily suggested. But Beevor held that serratus will not pull upon the scapula in trapezius paralysis until the deltoid raises the arm about 45 degrees from the side. Accordingly the girl has been instructed to secure this elevation of the arm by unobtrusively placing hand on hip, much in the style that a mannequin parades. The position is not used as a support for the arm, and she feels that the shoulder can more easily be braced back by this device. This case, compared with two similar, is a signal demonstration of the value to be derived from exercise in the increased mobility of the limb(48).

SUMMARY

In raising the arm from the side to the vertically upright position, from the very beginning to the very end of the action, there is continuous movement of the shoulder, scapulo-thoracic, acromio-clavicular and sterno-clavicular joints, and continuous activity of the associated muscles, whereas traditional teaching, by authors of repute, past and present, holds that abduction of the arm to the horizontal is secured by the full action of the deltoid causing complete movement of the shoulder joint, subsequent vertical elevation of the arm being made by trapezius and serratus rotating the scapula upon the chest while the humero-scapular angle remains constant.

It is an unusual procedure to radiograph the shoulder joint with the arm upright and one unknown to the anatomists and clinicians questioned, but a very graphic method of demonstrating the marked extent of the humero-glenoid movement in the second phase, in which half the joint movement occurs.

The behaviour of the scapula accordingly as the arm is abducted in the coronal plane or the plane of advanced abduction is explained.

The clinician, desiring a ready guide in estimation of the fully abducted shoulder joint, will observe that complete exhaustion of the joint movement is approximately indicated by the alignment of the humerus and the spine of

the scapula, Plate I, fig. 3, provided due allowance is made for individual variation.

As a rule, at the beginning of arm elevation, the inferior angle of the scapula makes an initial medial movement, but, in a few cases, it glides immediately lateralwards. As it is never stationary at the outset of arm elevation, the trapezius and serratus are accordingly never inactive. At the end of lowering the arm, there is a corresponding medial swing of the inferior angle of the scapula before it moves laterally again to the resting position. The normal activity of the trapezius and serratus upon the abducted arm is demonstrated by experiment, and the point is raised as to whether a muscle acts normally in the presence of a paralysed companion, and whether the defective movement resulting from a paralysed muscle presents a true analysis of its action as a component of the movement.

Exception is taken to the accepted statement: "The looseness of the capsule of the shoulder joint is so great that the arm will fall about 2·5 cm. from the scapula when the muscles are dissected from the capsule, and an opening made in it to counteract the atmospheric pressure."

The adequacy of a clinical method of estimating the shoulder-joint movement is questioned.

Various manipulative and radiographic experiments and a controversial review of the literature (particularly of the work of Duchenne, Cathcart, Cleland, Beevor and Wood Jones) are presented, together with certain side issues bearing upon the main theme.

Radiograms and photographs of a subject with trapezius paralysis are presented, showing that the scapula is higher, not lower, on the affected side, that there may be a peculiar jerk of the scapula in certain positions, without corresponding movement of the arm, and that the same continuous activity of the joints and muscles noted above practically holds good in elevation of the arm in the case of trapezius paralysis.

The condition and disposition of the muscles in trapezius paralysis are discussed.

Attention is drawn to the important part played by the weight of the limb and posture of the subject in normal and paralysed conditions, and the difficulties of relating the examination of an erect subject with a "recumbent" radiogram are illustrated.

I am indebted to Dr A. C. Fowler, radiologist to the Royal Aberdeen Hospital for Sick Children, for patient and indulging interest in the production of numerous radiograms.

EXPLANATION OF PLATES I–III

Plate I

Fig. 1. Male, 35 years, standing erect, plate anterior, right arm dependent.
Fig. 2. Male, 35 years, standing erect, plate anterior, right arm horizontal.
Fig. 3. Male, 35 years, standing erect, plate anterior, right arm vertical.
Fig. 4. Male, 35 years, supine, plate inferior. Loop strapped round right shoulder point and ischial tuberosity to prevent, as far as possible, scapular movement, while arm tries to secure vertical elevation.
Fig. 5. Wood Jones' diagram arguing that the angle of the scapula moves in the direction *A* with the action of the deltoid, and in the direction *B* with the action of trapezius and serratus magnus.
Fig. 6. Left trapezius paralysis, photograph of back, arms dependent.

Plate II

Fig. 1. Left trapezius paralysis, photograph of back, arms dependent, scapulae outlined upon skin, but movement of bones after the surface marking renders this approximate.
Fig. 2. Left trapezius paralysis, female, 19 years, standing erect, plate anterior, arms dependent, giving a general view of the shoulder girdles and thoracic skeleton, as far as possible upon a 15-inch plate.
Fig. 3. Left trapezius paralysis, standing erect, plates anterior, arms dependent, showing both shoulders upon separate plates, with the vertebral column incomplete. (Form of left glenoid cavity has been slightly altered in the retouching.)
Fig. 4. Left trapezius paralysis, supine position, arms by the side, showing both shoulders upon separate plates with the vertebral column incomplete.
Fig. 5. Left trapezius paralysis, photograph of back, with arms horizontal, before the scapula has dropped.
Fig. 6. The same as the above with the scapulae outlined.

Plate III

Fig. 1. Front view with arms horizontal, before affected scapula has dropped.
Fig. 2. Left trapezius paralysis, standing erect, plate anterior, arms horizontal, before scapula has dropped.
Fig. 3. Left trapezius paralysis, photograph of back with arms horizontal, after scapula has dropped, scapulae outlined.
Fig. 4. Left trapezius paralysis, standing erect, plate anterior, arm horizontal, after scapula has dropped.
Fig. 5. Left trapezius paralysis, photograph of back, with arms erect.
Fig. 6. The same as the above with the scapulae outlined.
Fig. 7. Left trapezius paralysis, standing erect, arm vertical, plate anterior; the coronal plane of the patient's trunk is not parallel to the plate, but slewed slightly so that the left side is nearer.

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Fig. 1

Fig. 2

Fig. 3

Fig. 4

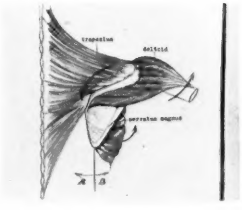

Fig. 5

Fig. 6

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Fig. 1

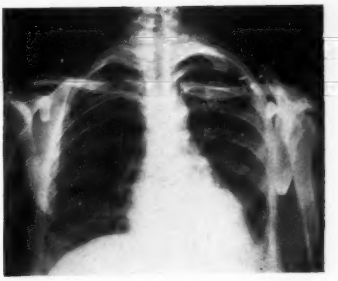
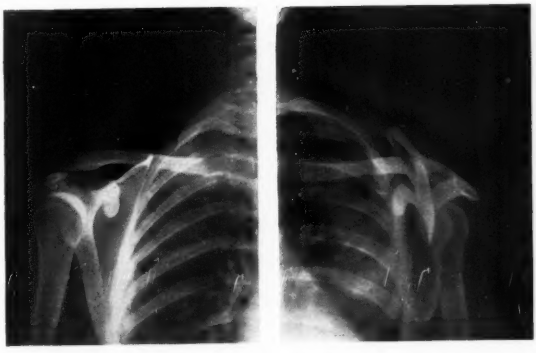


Fig. 2



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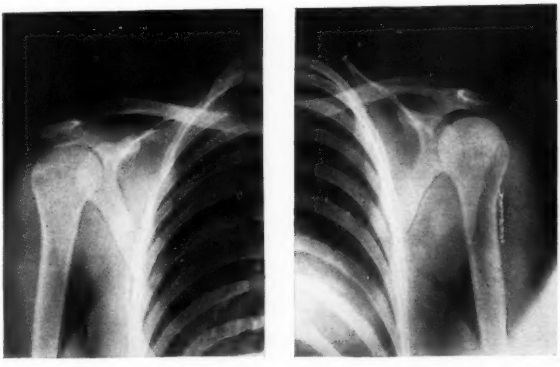

Fig. 4

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*(41) GAUPP (1894). *Centralb. f. Chir.*
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The humero-scapular and scapulo-thoracic joints (with 100 degrees and 45 degrees of movement respectively) are considered accessory, and the scapula is said to be practically stationary in the first part of arm elevation.

(44) FRAZER (1920). *The Anatomy of the Human Skeleton*, 2nd ed. p. 78.

In life the various actions of deltoid, trapezius and serratus are said to be practically synchronously combined. The text as far as it relates to the first phase agrees more or less with Cathcart and the present argument.

(45) HARROWER (1924). "Mechanical considerations in the scapulo-humeral articulation." *J. Anat.* vol. LVIII–LIX, pp. 222–7.

The discussion is on weight lifting to the horizontal, and the movement made by serratus and trapezius in abducting the arm to this level is not considered.

(46) BARDELEBEN (1904–13). *Handbuch der Anatomie des Menschen.*

Plate X, attached to the end of the third part of the second volume, II, 1, iii, 1911, shows outlines of the whole skeleton taken from radiograms, with the arms horizontal and vertical.

(47) CUNNINGHAM'S *Manual of Practical Anatomy* (1927), 8th ed.

Plate VI, fig. 56 *a*, opposite p. 127, shows a radiogram of the "shoulder region with the arm fully abducted," but the full movement of the shoulder joint has not been secured, because the arm is not vertical.

(48) NAUGHTON DUNN (1918). "The treatment of disabilities of the upper extremity in military surgery." *Brit. J. Surg.* vol. VI, No. 22, pp. 15–16.

Figs. 253 and 254 show remarkable range of scapular movement obtained with an ankylosed shoulder joint.

* I have not had access to the references marked by an asterisk.

CYSTIC OVARY IN A BABE AGED TWO MONTHS

By H. A. HARRIS, D.Sc., M.B., B.S.

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THE recent experimental work on the effect of pituitary extract on the growth of the genital system justifies the description of an ovary found post-mortem in a babe of two months. Death was due to broncho-pneumonia. No gross lesions of any urogenital or endocrine organs, other than that of the ovaries, were observed by Sir Bernard Spilsbury, to whom I am indebted for the specimen. The uterus and tubes, of normal size, were accompanied by large multi-locular cystic ovaries (fig. 1). The ovaries measured 2·6 cm. in length and

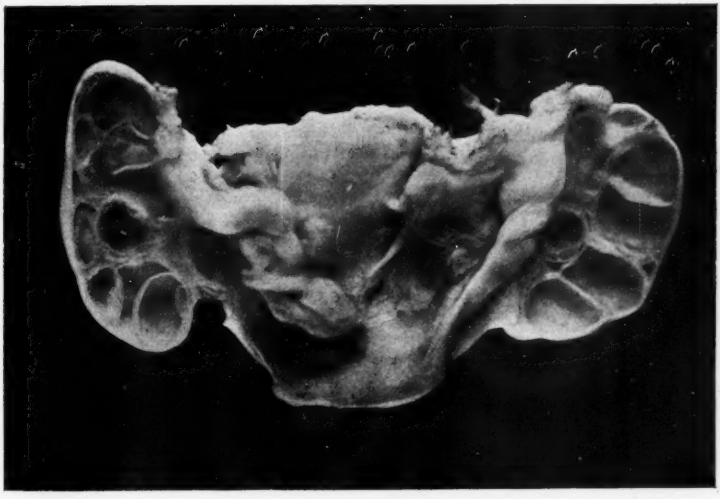

Fig. 1. The two cystic ovaries in section with the tubes and uterus. $\times 1\frac{1}{2}$.

were almost of adult size. On section the ovary presents a number of large cysts, containing a fluid resembling liquor folliculi.

On histological section the germinal epithelium is seen to consist of the typical cuboidal variety of cells. There is some trace of proliferation, and in occasional instances examination of serial sections shows continuity between the surface epithelium and the "egg tubes" of the cortex. The "egg tubes"

are numerous, indicating considerable activity in the formation thereof in the period before death, for large-celled ova have become differentiated from the smaller egg-tube cells to varying degrees, and the egg-tube cells differ but little from the cuboidal cells of the surface epithelium.

The cortex in its outer part is occupied by a connective tissue stroma in which the egg-tubes lie. The deeper layer of the cortex has numerous primary follicles, with an investment of satellite epithelial cells. Still deeper are a few secondary follicles in which an ovum is present, invested by a layer of four to six epithelial cells. There are several follicles which have proceeded further and entered upon the stage of formation of liquor folliculi.

The medulla, in two-thirds of its extent, is occupied by seven large cystic follicles (fig. 2) distended with fluid and contains several follicles which

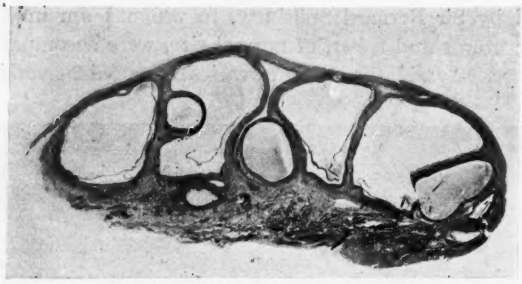

Fig. 2. Longitudinal section of the ovary showing the cysts. ×3.

collapsed during the handling of the specimen after death. There are several atretic follicles, and one of these is shown (fig. 3). The cytoplasm has a clotted appearance, and cells of the discus proligerus are invading it. Several follicles present the same phenomena of invasion of the cytoplasm of the ovum by the cells of the discus proligerus. Almost all the follicles show a separation of the area granulosa from the theca interna. Whether this is a post-mortem change or an abnormal relationship cannot be decided. Moreover, even in Gray's *Anatomy* it is stated that "the stratum granulosum may be separated from the external limiting membrane before the ovarian follicle bursts." Whether such a separation leading to freeing of the ovum is a normal preparation for the journey along the tubes or whether the separation is related to the lymph sinus of the atretic follicle described by Hill and Gatenby is doubtful.

It is difficult from the serial sections to reconstruct the life-history of a follicle in this ovary. Yet it would appear that cells of the discus proligerus may act as phagocytic cells in relation to the ovum, and there are evidences in the sections that the cells of the stratum granulosum exhibit a pseudo-lutein reaction. In certain areas the cells of the stratum granulosum have

proliferated presumably after death of the ovum, and simulated to some extent the formation of lutein cells. They have gradually died in the liquor, and the fine connective tissue cells between them have spread through the liquor. The membrana propria has become more distinct and the cells of the theca interna have undergone rapid proliferation with marked capillary formation. In several places there are collapsed areas of fine connective tissue bounded by larger connective tissue cells. The fine connective tissue core is derived from the delicate connective tissue of the stratum granulosum, and the larger cells on the boundary zone are developed from the theca interna. These areas can be traced in various stages up to the stage of a scar. Thus there is a pseudo-lutein reaction in the follicle and a process of fibrosis comparable to that seen normally in the formation of a corpus albicans.

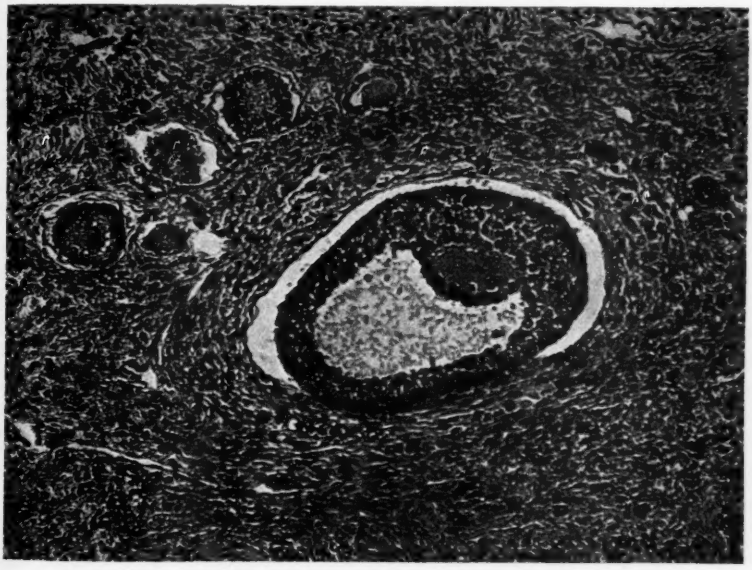

Fig. 3. Atretic follicle in the cystic ovary showing the separation of the stratum granulosum from the theca. × 165.

COMMENT

The genital system of the foetus displays certain departures from the somatic system as regards rate of growth. The uterus in particular shows a marked growth in the last foetal month. In the first month of post-natal life there is a definite involution of the uterus, comparable to that occurring in the suprarenal glands. The uterus decreases from 4 gm. at birth to 2 gm. at the fourteenth day. From this time on until the tenth year there is but little

growth. A similar cycle of rapid prenatal growth, followed by neo-natal involution, has been described for the uterus masculinus in the male.

In view of the fact that in the new-born, mastitis in the male, and vaginal discharge in the female are frequently seen; in view of the occasional appearance of an aseptic orchitis in the male and of cystic ovary in the female, it may be suggested that these conditions are due to an increased permeability of the placenta both to placental hormones and to maternal hormones in the last month of foetal life. The changes in the last month of uterine life, particularly the hyperaemia of the foetal uterus, suggest the influence of the placental or maternal hormone. The act of parturition itself may depend to some extent on the summation of the maternal and infantile hormones. The summation of the pituitrin of the mother and foetus may be associated with the initiation of uterine contractions.

These assumptions are not without some pathological parallels. For instance, it is well known that the gross manifestations of congenital syphilis are rarely, if ever, seen in a foetus under five months. In the routine examination of many still-born babes and abortions, the spirochaete of syphilis has not been found on examination of the foetal organs in any case under five months. Osteo-chondritis syphilitica has not been seen in the routine radiographic and histological examination of a series of 300 still-born children at University College Hospital in any foetus under five months. At this age, degenerative changes in the placenta, endarteritis, hyaline degeneration and calcification normally begin. It appears therefore that the permeability of the placenta to the spirochaete synchronizes with the initiation of these changes in the placenta. From this time onwards the permeability to the spirochaete and to other organisms and toxins seems to increase. This is well shown by the incidence of abortion in chronic renal affections and in acute infections such as malaria, pneumonia and scarlet fever. Ballantyne has summarised the known cases of intra-uterine infections and poisoning. In no case is there evidence of the disease or of the poison in the foetus of less than five months.

The suggestion is made that the permeability of the placenta to organisms, toxins, placental and maternal hormones is largely determined by the degree of infarction of the placenta. The processes involved in the ultimate infarction commence at the end of the fifth month. The territory involved by the obliterative endarteritis of the placenta determines the area of increased permeability. These areas serve as a suitable nidus for the growth of organisms, a fact which is particularly well shown by the distribution of gummata in organs and tissues which display senile or traumatic changes.

The relationship of placental infarction and placental permeability to the clinical signs of activity in the urogenital system of the new-born, as instanced by this case of cystic ovary, may admit of an experimental solution in laboratory animals.

NOTE

Since this case was described before the Anatomical Society of Great Britain and Ireland at the meeting of 3 May, and it was suggested that the cystic condition might be due to the increased permeability of the placenta to the maternal pituitary hormone, an account has been given by Earl T. Engle and Philip P. Smith (*Anat. Rec.* 1929, vol. XLIII, pp. 239–50) of the experimental production of cystic ovaries in the mature rat by the daily transplantation of fresh anterior pituitaries. The figure shown by these authors (*loc. cit.* p. 240) should be compared with fig. 2.

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COMMUNICATING BRANCHES BETWEEN THE CERVICAL SYMPATHETIC AND THE DESCENDENS CERVICALIS

By ALVARO RODRIGUES
Assistant of the Institute of Anatomy of the Faculty of Medicine of Oporto

In his description of the rami communicantes which arise from the superior cervical ganglion, Hovelacque, in his recent and well-known treatise[1], makes the following statement on p. 688: "Braeucker a vu une fois le ganglion cervical supérieur donner deux filets à la branche descendante du plexus cervical."

Such an anastomosis, far from being rare, as might be concluded from the foregoing quotation, is, on the contrary, in my experience quite common. My experience has been gained from dissections which I have systematically carried out for the past two years, in order to study the ansa hypoglossi and its branches.

A description of such communicating branches arising not only from the superior cervical ganglion, but also from the sympathetic system generally, is the subject-matter of this communication. My observations are based on the dissections of 45 bodies of which 26 were adults (19 male, 7 female), 1 female child four years old, and 18 foetuses (12 male and 6 female).

In 78 of these 90 cases I found very obvious connections of the sympathetic with the descendens cervicalis. These connections consisted mainly of filaments, arising either from the superior cervical ganglion or from some of its branches.

They were represented in 13 cases by filaments, which arising from the superior cervical ganglion or from the rami communicantes to C II or C III, join the loop between these two cervical spinal nerves, close to the origin of one or more of the roots of the descendens cervicalis nerve.

In other cases one or all of the roots of the descendens cervicalis derived from C II and from its ramus communicans arose in such manner that the descendens cervicalis frequently appeared to be derived from the ramus communicans to C II only.

For convenience sake, I shall describe six fundamental types of these anastomoses, which may be classified as follows:

(1) Branches from the superior cervical ganglion.

(2) Branches from the ramus communicans to C II.

(3) Branches from the ramus communicans to C III.

(4) Branches from a ramus communicans joining the loop between C II and C III.

[1] Hovelacque, *Anatomie des nerfs craniens et rachidiens et du système grand sympathique*, Paris, 1927.

(5) Filaments joining the loops between the cervical spinal nerves, or joining these nerves, close to the points whence arise the roots of the descendens cervicalis nerve.

(6) The ramus communicans to C II being so closely associated with one or more roots of the descendens cervicalis arising from C II, that it may be regarded as assisting in their formation.

I. BRANCHES FROM THE SUPERIOR CERVICAL GANGLION

In 13 out of 90 cases, filaments from the superior cervical ganglion formed the descendens cervicalis (9 adults, all on the left side, and 4 foetuses—3 male and 1 female, all on the right side). In most cases (11) the communicating filament was short, single, and passed obliquely from the ganglion to the root of the descendens cervicalis, which arose, either from the loop between C II and C III, or from C II, and joined the root of the descendens cervicalis at a point distant from its origin between 1 to 5 mm. in the foetuses, and between 5 mm. to 3 cm. in the adults.

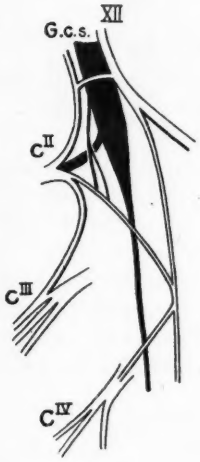

Fig. 1

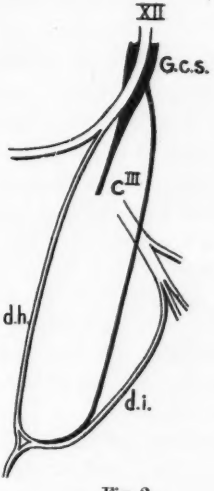

Fig. 2

In the case represented in fig. 1 (on the right side of a female foetus) the communicating filament bifurcated, and the two resulting branches both joined the same root of the descendens cervicalis. In another case (on the left side of the neck of João, R. V., aet. 59 years) the branch from the superior cervical ganglion to the descendens cervicalis was joined by a communicating branch from the ramus communicans to C III.

When this communicating branch to the descendens cervicalis was present the rami communicantes proper to C II and C III arose separately from the

superior cervical ganglion, and as a rule the communicating branch arose from the ganglion intermediately between the two rami.

In two cases, however (as represented in fig. 1), the communicating branch to the descendens cervicalis arose from the ganglion above the ramus communicans to C II, and crossed its anterior surface.

In one case (the left side of the neck of Joaquina, A., aet. 4 years, fig. 2), the communicating branch was long and almost as thick as the descendens cervicalis itself; it arose from C III; first descended in the neck deeply to the internal jugular vein and the common carotid artery and then came into close contiguity with the descendens cervicalis at the point where this branch came into relation with the external aspect of the internal jugular vein. It accompanied the descendens for a short distance with a mutual interchange of fibres, and finally joined the descending ramus of the hypoglossal nerve independently and with it formed a small loop with its concavity directed upwards.

II. BRANCHES FROM THE RAMUS COMMUNICANS TO C II

Out of the 90 cases observed 17 conformed to this type: 9 in adults (4 on the right, 5 on the left), 8 in foetuses (4 on the right, 4 on the left).

Fig. 3 represents a typical case.

The ramus communicans to C II, at a variable point in its course, generally at or about its middle, gives off a branch, of variable thickness, which, at a lower level, joined one of the roots of the descendens cervicalis, a root that in 9 cases arose from C II, and in 7 from the loop between C II and C III.

In a male foetus with club-feet[1], the communicating branch to the descendens cervicalis arose on the right side from the ramus communicans to C II, near the point where the ramus was given off from the superior cervical ganglion, a condition which may be regarded as transitional between Class I and Class II.

In another foetus (a female), the communication arose on the right side from one of the rami communicantes to C II, and after a short vertical course bifurcated. Of the two branches resulting from the bifurcation the internal joined a root of the descendens cervicalis arising from the loop between C II and C III; the external joined a second root of the descendens cervicalis arising from C III.

III. BRANCHES FROM THE RAMUS COMMUNICANS TO C III

In 4 cases out of the 90 observed, a communicating branch to the descendens cervicalis arose from the ramus communicans to C III. As the dispositions in the four cases were not identical, each one of the four merits a special brief description.

[1] This foetus was one of triplets (*vide* Hernâni Monteiro, "Deux cas de grossesse multiple," in *Folia Anatomica Universitatis Conimbrigensis*, 1928).

In the case represented by fig. 4, the right side of a full-time male foetus, the communicating filament was 3 cm. long, arose from the ramus communicans to C III, some little way above the point where the ramus joined C III, and descended almost vertically, on the outer side of the descendens cervicalis[1], which it joined as the latter curved round on to the external surface of the internal jugular vein.

In the second case on the left side of Abilio, M. M., aet. 26 years, a similar disposition was exhibited by the communicating filament, but in this case the descendens cervicalis had 4 roots. Two of the 4 roots arose from C III, and one of these was joined by the communicating filament.

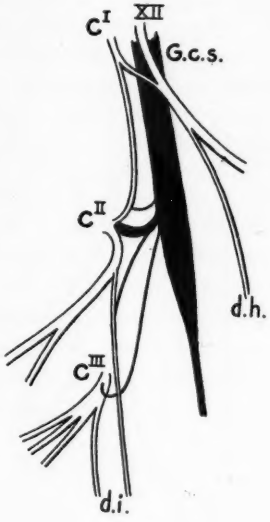

Fig. 3

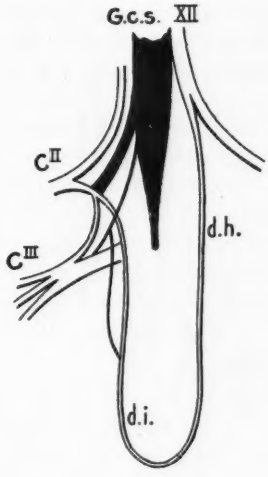

Fig. 4

In the third case (on the right side of a full-time female foetus) the ramus communicans to C III arose in common with that to C II. The ramus communicans to C III bifurcated into two branches, one of which joined the descendens cervicalis.

The fourth case represented in fig. 8 was more complicated. In addition to a communicating filament from the ramus communicans to C III the root of the descendens cervicalis received other filaments of various origin. This case will be described in detail later with other special cases.

[1] The descendens cervicalis arose, by one root only, derived from the loop between C II and C III (fig. 4).

IV. BRANCHES FROM A RAMUS COMMUNICANS TO THE LOOP BETWEEN C II AND C III

Two cases of this type were observed.

Fig. 5 represents a case (on the right side in an adult) with two ansae hypoglossi. From the superior cervical ganglion, below the point whence the ramus communicans to C II arose, another ramus was given off and joined the loop between C II and C III. From the latter, 2 mm. below its origin from the ganglion, a communicating branch was given off, and after a short course outwards and downwards, joined the communicans cervicalis which arose from the loop between C II and C III and took part in the formation of the superior ansa hypoglossi.

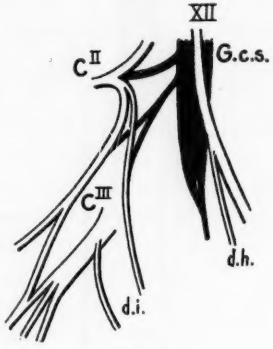

Fig. 5

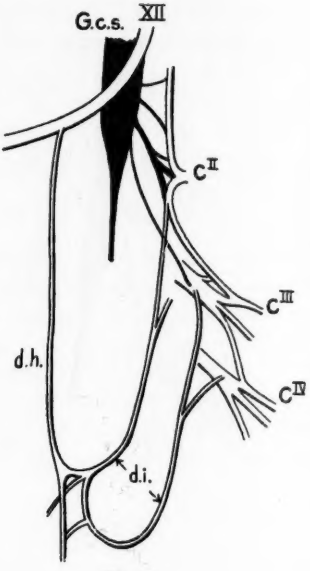

Fig. 6

Slightly different was the disposition observed on the left side in Ana, C., aet. 70 years. In this case the ramus communicans to the loop between C II and C III arose from the ramus communicans to C II. Two filaments of the branch to the loop between C II and C III joined the root of the descendens cervicalis which arose from the loop between C II and C III.

V.

In this group, and in the following, are included cases in which fibres arising from the superior cervical ganglion and joining directly or indirectly the descendens cervicalis, instead of being distinct branches, as in the cases already described, are closely associated with the rami communicantes to

C II or to C III or to the loop between C II and C III, whence the sympathetic fibres are given off to the descendens cervicalis close to the point where the roots of this nerve arise.

The most frequent disposition (9 times on the left, and 4 on the right) was the following: a branch of the ramus communicans to C II, or one arising independently from the superior cervical ganglion, joined the loop between C II and C III, nearly tangentially and at a point whence arose one of the roots of the descendens cervicalis, into which were prolonged the more internal fibres of the branch from the sympathetic.

Without it being necessary to tear the sheath of the nerve loop, I could frequently see the fibres of the sympathetic branch prolonged without interruption into the descendens cervicalis.

Another disposition which was observed in 10 cases (4 on the right, and 6 on the left) was the following: the ramus communicans to C III arose either from the ramus communicans to C II or directly from the superior cervical ganglion, and joined the spinal nerve, at the point at which one of the roots (usually the inferior) of the descendens cervicalis arose.

In two cases only did C III receive more than one ramus communicans from the superior cervical ganglion (on the right side of a full-time male foetus in which it received two, and in another in a full-time male foetus, also on the right side, in which it received three), and one of these rami communicantes, although co-existing with other forms of connection with the sympathetic, presented with the root of the descendens cervicalis a disposition similar to that described above, which confirms the relations of continuity of the fibres of the sympathetic with those of this root of the ansa hypoglossi.

VI.

I will now describe a disposition which I found several times.

It differed from the forms of connection already described, but in some cases co-existed with them. I observed it in 10 cases (6 on the left side, and 4 on the right).

Fig. 7 shows the disposition observed on the left side of a male foetus, and represents what I may term the fundamental type. From the terminal portion of the ramus communicans to C II or from the point at which this ramus communicans joined C II, one of the roots (nearly always the superior) of the descendens cervicalis arose.

From the direction of its fibres it could be seen that both the anterior division of C II and its ramus communicans contributed to the formation of this root.

Hovelacque[1], when describing the descendens cervicalis, refers to the origin of its roots as follows: "nous avons vu plusieurs fois la racine supérieure naître, non pas de la II^{e} paire cervicale, mais du gros rameau unissant la II^{e} cervicale au ganglion sympathique."

[1] Hovelacque, *op. cit.* p. 362.

I found that the most frequent disposition of the connection between the sympathetic and the descendens cervicalis, in cases where more than one root of the latter nerve existed, was that one root only of the descendens cervicalis, and this almost invariably the superior, received fibres from the sympathetic.

However, I met cases which proved an exception to this rule. Such a case is represented by fig. 6, in which each branch of the descendens cervicalis was connected with the ramus communicans to the spinal nerve from which it took origin.

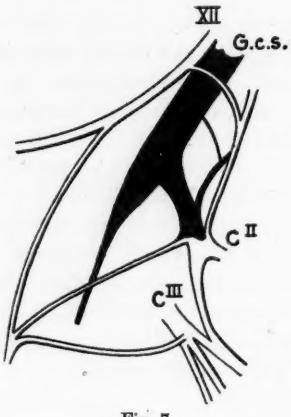

Fig. 7

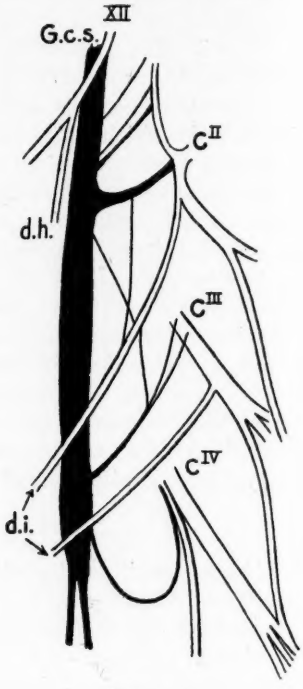

Fig. 8

In other cases I found that a root of the descendens cervicalis received two or more communicating filaments of the sympathetic, from the same or from different sources. Fig. 8, which represents the condition found on the left side in Fernando, G., aet. 30 years, deserves special description. It was a case of double ansa, in which the root of the superior ansa arose from the inferior branch of bifurcation of C II. From the upper part of the superior cervical ganglion, which was about 11 cm. long, and slightly constricted 2 cm. above its lower end, were derived three rami communicantes to the loop between C I and C II. Given off a little lower down, another thicker ramus joined the point of bifurcation of C II, from which a filament passed downwards

and joined an upper descendens cervicalis derived from C II, 2 cm. below its origin. From the inferior portion of the ganglion were derived two rami communicantes, one joined C IV, the other passed upwards and trifurcated into three filaments, one of which joined the upper descendens cervicalis, derived from C II, while the remaining two joined the trunk of C III and represented a double ramus communicans to this spinal nerve.

From the superior cervical ganglion was derived yet another filament which arose 1 cm. below the origin of the ramus communicans to C II, and again joined the upper descendens cervicalis derived from C II.

Consequently the upper descendens cervicalis derived from C II and concerned in forming a superior ansa, received three communicating filaments from the sympathetic: one from the superior cervical ganglion, a second from the ramus communicans to C II, and a third from that to C III. The last-mentioned, in its disposition was somewhat like the one referred to by Hovelacque[1], who described a second ramus communicans to C III, which, independently of the one from the superior cervical ganglion, may be derived from the middle cervical ganglion: "Lorsque ce second rameau de la III^{e} paire existe, il se porte obliquement en haut et en dehors sur le grand droit antérieur, il se jette sur le 3^{e} nerf juste en dehors de l'intertransversaire antérieur, parfois il se jette sur la racine inférieure de la branche descendante du plexus cervical ou sur la racine du phrénique."

In my case the ramus communicans to C III was unique, or presuming it represented a double ramus, sprang by a single trunk from the superior cervical ganglion; but its course and the constriction of the ganglion (undoubtedly representing a coalescence of the middle and the superior cervical ganglia) make my case similar to that of Hovelacque.

In addition to the cases already described I found others, in which, owing to the complex morphology of the branches of the ansa, the communicating branches from the sympathetic exhibited very different dispositions.

Fig. 9 represents the disposition found on the right side of a female foetus. A double ansa lying behind the internal jugular vein was present. A superior cervicalis descendens which formed the superior ansa arose, by one root only, from the point of division of C II, close to the point where the spinal nerve was joined by its ramus communicans. The superior cervicalis descendens passed downwards and inwards to meet the descending ramus of the hypoglossal nerve, and in so doing crossed obliquely the ventral aspect of the superior cervical ganglion of the sympathetic with which it exchanged such a large number of fibres that it was impossible to separate the ganglion from the nerve. This case should be considered as one of real fusion between the superior cervical ganglion and the descendens cervicalis, without the latter losing its individuality completely.

A still more remarkable case was the disposition observed on the right side of a male foetus (fig. 10). In this case the descendens cervicalis was replaced

[1] Hovelacque, *op. cit.* p. 347.

by a branch given off from the vagus at the level of the hyoid bone. From the superior cervical ganglion sprang a large thick branch which joined C II, and in addition, a much smaller branch passed upwards and joined the upper end of the loop between C I and C II, close to the point whence emerged a communicating branch from the loop to the vagus nerve; some sympathetic fibres could be seen passing without interruption from the sympathetic twig to the communicating branch and thence to the vagus.

This branch of the superior cervical ganglion obviously represented the communicating filaments, already described, from the sympathetic to the descendens cervicalis, since the origin of the descendens cervicalis from the vagus was apparent rather than real, the true descendens cervicalis being represented by the communication from the loop between C I and C II to the vagus; its fibres being bound up in the sheath of the vagus for some distance

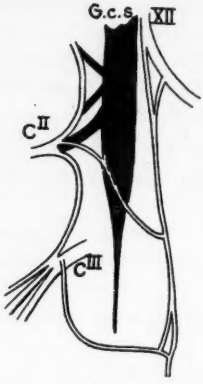

Fig. 9

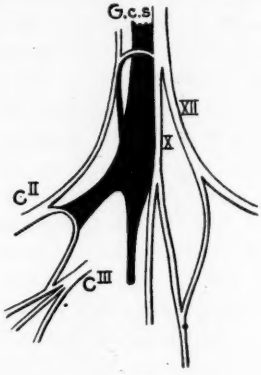

Fig. 10

before parting company with it to join the descending branch of the hypoglossal and complete the ansa hypoglossi. This abnormal descendens cervicalis conveyed sympathetic fibres which reached it *via* the branch from the superior cervical ganglion to the loop between C I and C II and thence by the communication from the loop to the vagus.

In addition to the cases in which the association of sympathetic filaments with the roots of the descendens cervicalis were easily visible, I observed others in which such association did not exist. In the course of my dissections I frequently observed filamentous branches from the superior cervical ganglion (smaller than the rami communicantes to C II and C III, and independent of them) which joined the loop between C II and C III, and to these branches I paid particular attention.

Searching through the literature on the subject, e.g. Cruveilhier, Sappey, Hovelacque, Bishop Harman[1] amongst others, I found that little or no

[1] Bishop Harman, "The anterior limit of the cervico-thoracic visceral efferent nerves," *J. Anat. and Physiol.* (1900), vol. xxxiv, pp. 357–80.

notice had been taken of these branches of the superior cervical ganglion[1]. Hovelacque[2] makes the following statements: "Deux ou trois filets grêles, presque transversalement dirigés, se terminent prévertébraux en se jetant sur l'arc de l'atlas. Au-dessous d'eux un très gros rameau, constant dans son existence, décrit une courbe à concavité supérieure, pour se jetter dans l'angle de bifurcation de la branche antérieure du deuxième nerf cervical. Plus bas, un rameau oblique en bas et en dehors, gagne la branche antérieure du troisième nerf cervical."

The results of my own observations on the branches of the superior cervical ganglion to the loop between C II and C III are as follows. Apart from those cases where the ramus communicans to C II, which can always be recognised by its relatively large size, instead of having its normal disposition as described by the authors quoted above, joined the commencement of the inferior branch of bifurcation of C II, and also apart from those cases where the ramus communicans to C III is absent, I noted that in every case where a filament from the superior cervical ganglion to the loop between C II and C III was present one of the roots (the superior) of the descendens cervicalis also arose from the loop, either at the point where the loop was joined by the sympathetic filament or below it.

Further, in the cases in which the roots of the descendens cervicalis did not arise from the loop between C II and C III, a communicating filament from the superior cervical ganglion to the loop was absent, with the exception of those cases to which I have already referred where the ramus communicans to C III joined the upper end of the loop between C II and C III, and of those cases where the ramus communicans to C III was wanting.

In order to complete the study of the ansa hypoglossi, I dissected several animals, and in two cases I found sympathetic filaments with a disposition, similar to that found in Man.

Fig. 11 represents the disposition found on the left side of a *Lutra vulgaris* ♀. An ansa hypoglossi did not exist, but was represented by a branch arising from the bifurcation of C I, and supplying all the infra-hyoid muscles. This nerve to the infra-hyoid muscles received two communications from the sympathetic. An upper, a direct branch from the superior cervical ganglion which pursued a remarkably sinuous course, and a lower derived from the ramus communicans to C II. As this ramus communicans passed downwards to reach the spinal nerve it crossed the ventral aspect of the nerve to the infra-hyoid muscles.

The other case was observed on the left side of a Fox ♀. The nerve representing the descendens cervicalis, which joined a descending branch of the

[1] Concerning the grey rami from the superior cervical ganglion to the nerves of the cervical plexus, Morris Axford states that they are usually three in number; the middle ramus joining either C II or the loop between C II and C III (Morris Axford, "Observations on the cervical sympathetic in Man," *J. Anat.* vol. LXII, p. 301).

[2] Hovelacque, "Les rameaux communicants du sympathique cervical," *Annales d'Anatomie Pathologique Médico-Chirurgicale*, 1924, Tome I, p. 608.

hypoglossal nerve to form the ansa, arose from C I by one root only, and received, 1 cm. below its origin, a sympathetic filament, of some appreciable

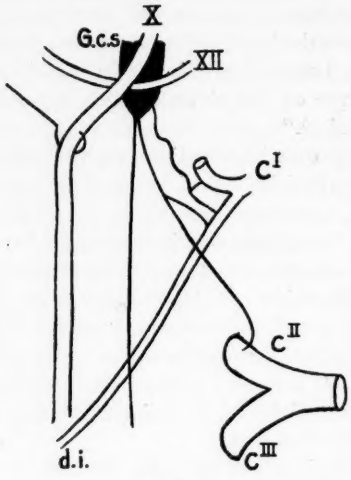

Fig. 11

size, from the lower end of the superior cervical ganglion. The sympathetic branch from the superior cervical ganglion to the descendens cervicalis co-existed with a ramus communicans to C I which joined this cervical spinal nerve, near its bifurcation.

KEY TO ILLUSTRATIONS

C I	First cervical nerve.
C II	Second cervical nerve.
C III	Third cervical nerve.
C IV	Fourth cervical nerve.
X	Vagus nerve.
XII	Hypoglossal nerve.
G.c.s.	Superior cervical ganglion of the sympathetic.
d.h.	Descendens hypoglossi.
d.i.	Descendens cervicalis.

FURTHER STUDIES OF THE CONDUCTING SYSTEM OF THE BIRD'S HEART

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INTRODUCTION

The histological investigation of the conducting system of the hearts of a number of the smaller birds, undertaken by the present writer (*J. Anat.* Jan. 1930), revealed that the specialised elements of this system comprise the following:

(*a*) *Sinu-auricular node*, situated beneath the epicardium at the base of the right venous valve, its specialised fibres being continuous with the neighbouring auricular myocardium and with the subendocardial Purkinje fibres in the vicinity.

(*b*) *Sub-endocardial Purkinje network* of both auricles, from which Purkinje fibres penetrate into the depth of the auricular myocardium around the branches of the coronary arteries, reaching in some places to the sub-epicardial connective tissue, and establishing continuity with the auricular myocardium. Neither the sub-endocardial nor the periarterial Purkinje fibres of the auricles form any specialised connections with the ventricular muscle (ordinary or specialised).

(*c*) *Auriculo-ventricular node*, situated in the lower and posterior part of the auricular septum, immediately to the left of the opening of the left superior vena cava, its specialised fibres being continuous below with the auriculo-ventricular bundle and with the right auriculo-ventricular Purkinje ring, and above with the ordinary auricular myocardium but not with the auricular Purkinje fibres.

(*d*) *The auriculo-ventricular bundle* passes from the lower end of the auriculo-ventricular node through the posterior part of the right auriculo-ventricular fibrous ring (near the posterior septal attachment of the muscular right auriculo-ventricular valve), where it lies just beneath the endocardium. Thence it is prolonged forwards, downwards and to the left into the depth of the ventricular septum, in which, midway between its right and left surfaces and about one-quarter of the distance from the base to the apex of the septum, the bundle divides into its right and left limbs. This site of the bifurcation of the bundle is just below and to the right of the anterior septal attachment of the muscular valve. The rounded right limb and the broad flattened left limb approach the endocardium on the corresponding sides of the ventricular septum, where they spread out to become continuous with the sub-endocardial

Purkinje network on either side of the septum. The right limb, as it approaches the endocardium, gives off a small branch which runs upwards and to the left, immediately beneath the endocardium, to enter the muscular valve at its anterior septal attachment. The main auriculo-ventricular bundle and its right and left limbs are not enveloped by a well-defined fibrous sheath, the specialised fibres being in direct apposition to and establishing continuity with the neighbouring septal myocardium.

(*e*) *Sub-endocardial Purkinje network* of both ventricles, from which Purkinje fibres penetrate through the thickness of the septal and free walls of the ventricles around branches of the coronary arteries, following in their course the "pattern" of the myocardial branches of the coronary arteries, reaching in some places to the sub-epicardial connective tissue, and establishing continuity with the ventricular myocardium. The ventricular sub-endocardial and periarterial Purkinje networks form no direct connections with the auricular muscle (ordinary or specialised).

(*f*) *Recurrent branch* of the auriculo-ventricular bundle, given off at the bifurcation of the main bundle, running upwards and to the left in the depth of the ventricular septum, in front of the mitral orifice, and finally in the connective tissue on the left side of the root of the aorta, where it inclines backwards to join the aortic end of the right auriculo-ventricular Purkinje ring behind the root of the aorta.

(*g*) *Right auriculo-ventricular Purkinje ring*, commencing from the lower and posterior part of the auriculo-ventricular node and running round the right auriculo-ventricular orifice in the connective tissue between the auricular and ventricular myocardial components of the muscular valve, finally joining the recurrent branch of the main auriculo-ventricular bundle behind the root of the aorta. On its way round it establishes continuity with the auricular and ventricular myocardial components of the muscular valve.

PRESENT WORK

In the present work an attempt has been made to display some of these elements of the specialised avian conducting system by dissection in the heart of a large bird, namely the ostrich. Three ostrich hearts were available for study, all previously fixed in formalin. The first heart was cut into a series of transverse horizontal slabs, each rather less than half an inch in thickness. The cut surfaces of the ventricular septum were examined, but the main auriculo-ventricular bundle could not be identified with any degree of certainty by the naked eye. By a careful examination with the dissecting microscope of the precise localities in which the auriculo-ventricular bundle had been found in the previous histological study, it was just possible to distinguish the slightly paler bundle from the neighbouring septal myocardium. The bundle was separated by blunt dissection from the cardiac muscle in each slab of the upper part of the ventricular septum and thus traced through the successive slabs upwards to the posterior part of the junction of the right auricle and

ventricle, where it lay just beneath the endocardium, and downwards to its bifurcation in the depth of the septum, whence the rounded right limb and the broad flat left limb were traced to the endocardium on the corresponding sides of the septum. The bifurcation of the bundle was situated about one-quarter of the way down the ventricular septum, and it lay midway between the right and left surfaces of the septum. In the microscopic study of the conducting system of the hearts of smaller birds, it was noted that the main bundle and its divisions were not enveloped by a well-defined fibrous sheath, actual continuity being established between the peripheral specialised fibres of the bundle and the neighbouring cardiac muscle. In separating the bundle and its limbs from the septal myocardium in the slabs of the ostrich heart, it was found that the connection between the bundle and the neighbouring septal muscle was so intimate that fine strands of the bundle became torn out as the cardiac muscle was separated. Slab 6 contained the lower part of the auriculo-ventricular bundle, the bifurcation of the bundle and the commencement of the right and left limbs of the bundle. The upper surface of the slab (fig. 1) showed the bundle which has broadened out just above its bifurcation, and the lower surface (fig. 2) showed the bifurcation of the bundle and the commencement of the rounded right and flattened left limbs. Fig. 3 shows the right and left limbs of the bundle in slab 7, passing to the endocardium on the corresponding sides of the septum. Slabs 6 and 7 together comprise about the lower inch of the upper quarter of the ventricular septum. The broad flattened bundle just above its bifurcation (fig. 1) lies midway between the right and left surfaces of the septum, and its surfaces are parallel with those of the septum.

In the second and third hearts an attempt was made to dissect the auriculo-ventricular bundle and its two limbs *in situ*. By superimposing the slabs of the first heart, in which the bundle and its divisions had been defined, a good guide to the topography of the bundle was obtained for the dissection of the other hearts. Dissection of the bundle *in situ* proved to be a long and careful task, the dissecting microscope being almost constantly employed, owing to the fact that the septal myocardium had to be removed piecemeal to approach the bundle in the depth of the ventricular septum, and also because, as was the case in the separation of the bundle from the myocardium in the heart slabs, when removing the cardiac muscle immediately adjacent to the bundle, the delicate bundle was easily damaged and fine strands of the bundle became torn out with the separated myocardium.

In the second heart the following parts of the avian-conducting system were defined: lower part of the auriculo-ventricular node, the main auriculo-ventricular bundle and its right and left limbs, and the commencement of the recurrent branch of the main bundle (fig. 4). In the third heart, in addition to the above elements, the commencement of the right auriculo-ventricular Purkinje ring from the lower and posterior aspect of the auriculo-ventricular node was also defined (fig. 5). The auriculo-ventricular bundle, when dissected out, takes the form of a delicate, pale, ragged, semi-translucent band, its ragged

appearance being due to unavoidable tearing in the process of dissection owing to the intimate connection of the bundle and the septal myocardium. The upper part of the bundle is rounded, but near its bifurcation it broadens out into a flattened band (the surfaces of which are parallel to the surfaces of the ventricular septum). It commences from the lower end of the auriculo-ventricular node in the connective tissue of the posterior part of the right auriculo-ventricular fibrous ring, close to the posterior septal attachment of the muscular right auriculo-ventricular valve. Here it lies just beneath the endocardium. Thence it passes forwards, downwards and to the left into the depth of the ventricular septum, until it attains a position about one-quarter of the way down the septum, a little below and to the right of the anterior septal attachment of the muscular valve. Here it lies midway between the right and left surfaces of the ventricular septum and divides into its right and left divisions. The right limb is small and rounded and passes to the right side of the septum, where it broadens out beneath the endocardium. The left limb is broad and flat and passes to the endocardium on the left side of the septum. From the left side of the bifurcation of the main auriculo-ventricular bundle a small round recurrent branch is given off, which passes upwards and to the left in the depth of the ventricular septum. It is the commencement of the recurrent branch of the main bundle which was traced in the previous microscopic study to the root of the aorta. From the posterior aspect of the lower end of the auriculo-ventricular node a small round bundle is given off, which runs into the connective tissue between the auricular and ventricular myocardial parts of the muscular valve at its posterior septal attachment. It is the commencement of the right auriculo-ventricular Purkinje ring.

These macroscopic dissections of parts of the avian-conducting system form an interesting corroboration of the reconstruction of these parts of the system in the previous histological study. Microscopic sections were made of many parts of the dissected system and showed the typical Purkinje structure. Fig. 6 is a micro-photograph of a piece of the dissected bundle. It shows that, although in this large heart there is some connective tissue about the Purkinje elements, there is not the same well-defined fibrous sheath such as is found in the large mammalian heart. The intimate relation of the Purkinje to the ordinary cardiac muscle is also seen.

It is well known that the sub-endocardial Purkinje network is visible to the naked eye through the ventricular endocardium in the larger mammalian hearts. In the ostrich heart the network can also quite readily be recognised through the ventricular endocardium, as a fine pale network beneath the endocardium. A strip of endocardium from the free wall of the right ventricle of the ostrich heart was dissected off and on staining showed that the visible network consisted of Purkinje fibres.

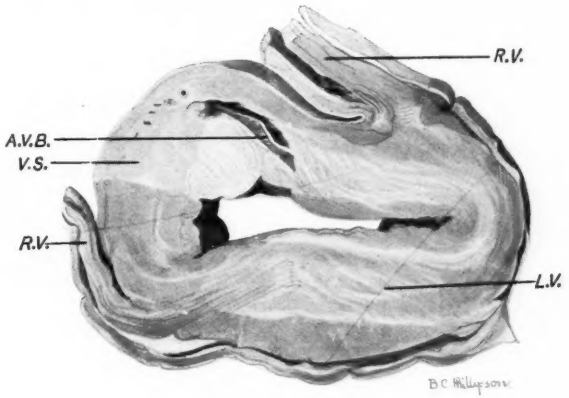

Fig. 1

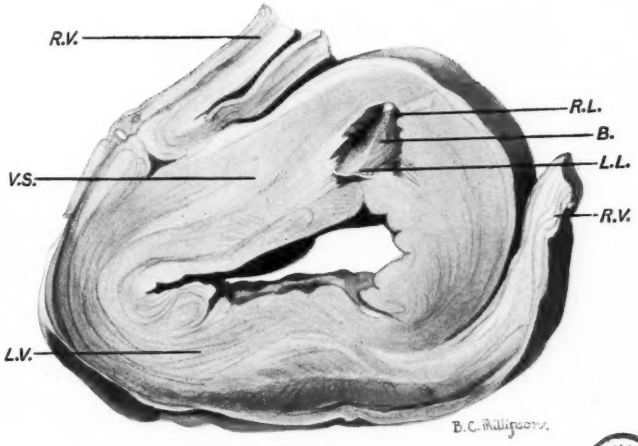

Fig. 2

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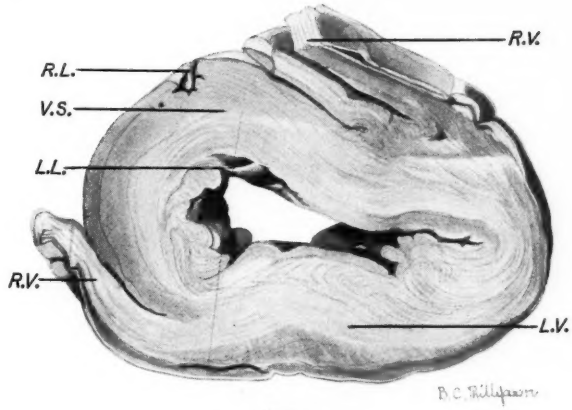

Fig. 3

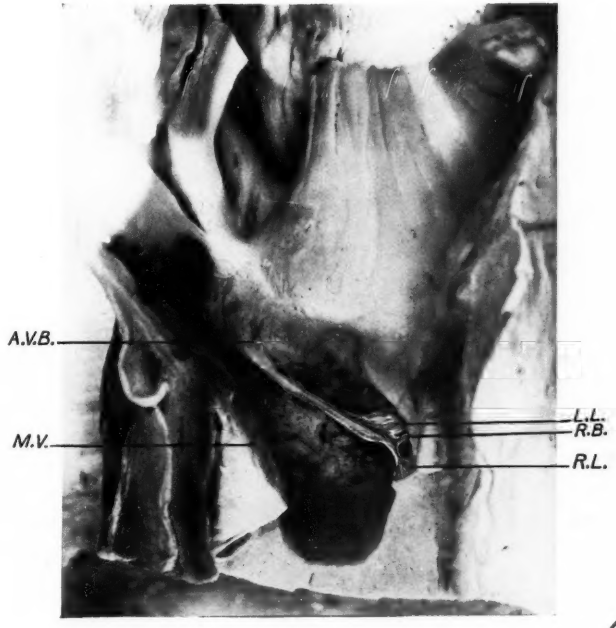

Fig. 4

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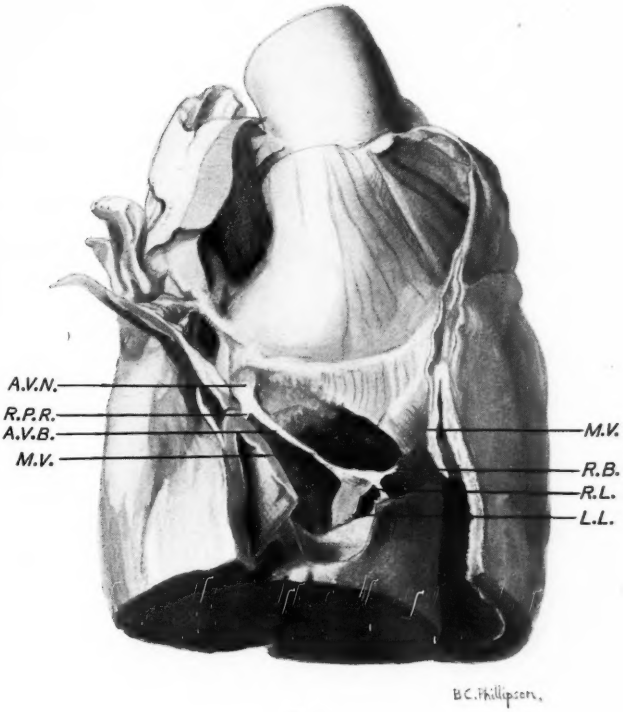

Fig. 5

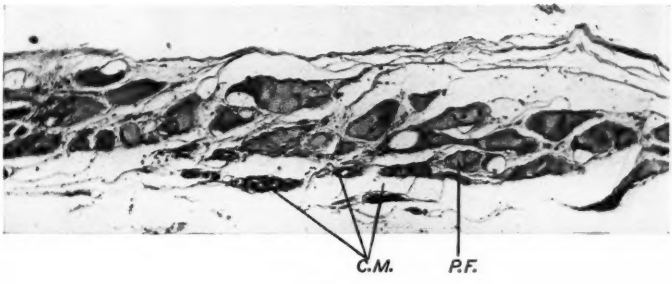

Fig. 6

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SUMMARY AND CONCLUSIONS

The gross dissection of certain parts of the specialised avian-conducting system corroborates the topographical reconstruction of these parts of the system, and the intimate connection of the specialised elements of the main parts of the system with the neighbouring myocardium, as determined in a previous microscopic study. Attention is also drawn to the visible sub-endocardial ventricular Purkinje network.

I wish to express my gratitude to Sir Thomas Lewis for his interest and suggestions for future work. My anatomical and histological researches afford significant corroboration of the results obtained in his electrical studies of the bird's heart. (*Phil. Trans. Roy. Soc.* 1916, vol. CCVII, B.)

DESCRIPTIONS OF PLATES I–III

PLATE I

Fig. 1. Upper surface of slab 6.
Fig. 2. Lower surface of slab 6.

PLATE II

Fig. 3. Upper surface of slab 7.
Fig. 4. Dissection of auriculo-ventricular bundle *in situ*.

PLATE III

Fig. 5. Dissection of auriculo-ventricular bundle *in situ*.
Fig. 6. Micro-photograph of section of auriculo-ventricular bundle.

ABBREVIATIONS USED IN FIGURES

A.V.B. Auriculo-ventricular bundle.
A.V.N. Auriculo-ventricular node.
B. Bifurcation of auriculo-ventricular bundle.
C.M. Cardiac muscle.
L.L. Left limb of auriculo-ventricular bundle.
L.V. Left ventricle.
M.V. Muscular valve.
P.F. Purkinje fibres.
R.B. Recurrent branch of auriculo-ventricular bundle.
R.L. Right limb of auriculo-ventricular bundle.
R.P.R. Right Purkinje ring.
R.V. Right ventricle.
V.S. Ventricular septum.

CRANIOMETRIC MEMOIRS

No. II. THE HUMAN AND COMPARATIVE ANATOMY OF CAMERON'S CRANIO-FACIAL AXIS

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In 1924 the writer (1) brought forward evidence to show that the human basis cranii became bent upon itself during the early stages of intra-uterine life. It was ascertained that this cranial flexion occurred in the region of the pituitary fossa. As a result, he showed that the cranial base became very conveniently divided into pre-pituitary and post-pituitary segments. It was thus clear that, as the process of cranial flexion advanced, these two segments gradually formed an angle with each other. The latter was termed by the writer "the angle of cranial flexion." His next duty was to discover the approximate location of the salient of this angle. As this meant the creation of a new "craniometric point," the writer decided to give the problem very careful study. As a matter of fact, three locations were open for consideration, namely, the anterior edge, the posterior edge and the bottom of the pituitary fossa. The latter was at once ruled out of court as offering nothing definite. The posterior edge was also found to present objections, chiefly on account of its relative degree of development in different crania, due apparently to the varying size of the posterior clinoid processes. Of course the influence of the attachments of the tentorium cerebelli upon the configuration of the latter could be well understood and appreciated. Thus by a process of exclusion the anterior edge of the pituitary fossa alone remained for consideration. The writer has given reasons in previous papers for selecting this as the "pituitary point," and has also described its features in Man (2) and in lower Mammals (4). It will therefore be unnecessary to dilate further upon this topic in the present communication.

In the first-mentioned paper (1) the writer directed attention to the fact that the pituitary point possessed certain advantages over Huxley's prosphenion point as the salient of the cranio-facial axis. The chief of these was, that the pituitary point represented approximately the site where that axis became bent upon itself, whereas the prosphenion point was really some distance in front of this. Another serious objection to the cranio-facial axis devised by Huxley was that its posterior segment was not in the line of the cranial base at all. The author agrees with Huxley that the basion is the most satisfactory and indeed essential point to represent the posterior end of the axis. On the other hand, the selection by Huxley of the nasion as its anterior extremity is more open to question. For example, the writer has shown in a

recent paper (9) that "the position of the nasion was found to display the usual ranges of variation that are associated with all craniometric points." He then went on to show that one disturbing factor was the propinquity of the frontal sinuses particularly in the Negro races. He also found that there was a sexual factor which determined the position of the nasion. In spite of these manifest drawbacks the writer sees no valid reason for departing from Huxley's recommendation to utilise the nasion. It certainly can be located with ease, and, moreover, it is situated at the junction of the cranial with the facial portion of the skull, a fact which probably prompted Huxley to adopt the term "cranio-facial axis." There is, it must be confessed, no other cranial point in the vicinity that suggests itself to the writer as a suitable substitute for the nasion. He considered the plane of the ethmoidal cribriform plate as a possible means of indicating the pre-pituitary segment of the axis, but this had to be dismissed upon ascertaining that in lower Mammals it became strongly curved on itself to form the floor of the "olfactory pocket." The latter will be found described for the first time in the last section of this memoir.

As the present paper is to deal with the cranio-facial axis that was suggested by the writer, it will be necessary for him to make an explanatory statement to the effect that it consists of an anterior or pre-pituitary segment, which extends from the nasion to the pituitary point, and a posterior or post-pituitary segment extending from the pituitary point to the basion.

This memoir is founded upon research work that was conducted in the Hamann Museum, Western Reserve University. The writer therefore desires to express his most grateful thanks to Prof. Wingate Todd for the full use of the cranial material and equipment of that wonderful, and, in many respects, unique collection. The illustrative photographs were taken under Prof. Todd's direct supervision. The author also wishes to record his best thanks to Miss W. M. Kuenzel for the part she played in preparing the photographs and also for the skilful way in which she drew the lines representing the cranio-facial axis at his direction.

Mesially sectioned crania were of course a *sine qua non* for the purpose of this research. In addition to the human material, which will be referred to later, the Museum contained crania of the higher and lower anthropoids, the lemurs (including such a rare genus as *Tarsius*) and the Carnivora. The writer is greatly indebted to Dr J. M. Ingersoll for the use of the orang and gibbon skulls. As all these lower mammalian types were represented in the Museum by only one mesially sectioned cranium for each genus, it is necessary to state that the relationship of the two segments of the cranio-facial axis to one another as found in these genera must not be regarded as indicating the average condition. For example, the size of the angle formed between the two segments of the axis, as well as the relative proportions of these segments, were found to exhibit in the four groups of human crania the usual wide ranges of variation that are associated with all cranial measurements. It was therefore natural to assume that these ranges would also be exhibited by the crania of all the

orders of the Mammalia. It follows that the time when whole series of mesially sectioned crania, representing each of the lower mammalian types, are available for estimating, averages will have to be relegated to the distant future.

RANGES OF VARIATION AND STANDARD DEVIATIONS OF THE PRE-PITUITARY SEGMENT OF THE CRANIO-FACIAL AXIS IN THE HAMANN MUSEUM WHITE AND NEGRO CRANIA

The writer has just been referring to that great bugbear of craniometry, namely, the range of variation. It is therefore appropriate to discuss at this stage the ranges of variation of the pre-pituitary segment. In the male White crania the maximum was 73·0 mm. and the minimum 50·5 mm., the actual range being thus as much as 22·5 mm. The range was slightly less in the male Negroes. In this case the maximum was 68·0 mm., and the minimum 51·5 mm., the range being 16·5 mm. The existence of this racial difference was found to be confirmed by the female crania. For instance, the maximum in the female Whites was 66·0 mm., and the minimum 50·5 mm., the range being therefore 15·5 mm. In the female Negro crania, on the other hand, it was slightly less, namely 14·0 mm., the maximum in this case being 66·0 mm., and the minimum 52·0 mm.

When making a comparison of the standard deviations of cranial measurements in different cranial groups, the writer's experience has shown that each of these groups should be represented by an equal number of crania. Moreover, he has ascertained that each group should be represented by a minimum of fifty crania. If hundreds are available, then so much the better, as by such means the standard error becomes considerably reduced. With these precautionary measures much more balanced comparisons are likely to result. The male White and male Negro crania in the Hamann Museum are abundant, but the female series falls very much short of these. Thus the writer found that exactly sixty female Negro crania were available for the particular purposes of this investigation. In view of what has just been stated, he therefore decided to limit the other three groups, namely, the male White, the female White and the male Negro crania, to the same number. This meant that a total of two hundred and forty human crania had to be studied.

The standard deviations of the pre-pituitary segment of the cranio-facial axis proved to be closely similar in all four groups of crania. For instance, it was 3·16 for the male White crania and 3·21 for the male Negro crania, the racial difference being thus fractional. The standard deviation for the female Negro group was almost exactly the same as that for the male Negroes, the actual figure being 3·19. The standard deviation was found to be highest in the female Whites, with 3·50. The coefficients of variability, as usual, followed these results consistently. The various calculations are displayed in Table I, which also shows the standard errors. It may be noted that the standard deviations in Table I differ fractionally from those calculated for other groups of Hamann Museum crania (6).

Table I

The standard deviations of the pre-pituitary segment of the cranio-facial axis are closely similar in the Hamann Museum White and Negro crania, the racial difference being merely fractional.

	Standard deviations	Coefficients of variability
Male White	3·16 ±0·1946	5·17 ±0·3184
Male Negro	3·21 ±0·1977	5·39 ±0·3320
Female White	3·50 ±0·2156	5·98 ±0·3683
Female Negro	3·19 ±0·1965	5·54 ±0·3412

The writer has shown in a previous paper (7) that the average length of the pre-pituitary segment of the cranio-facial axis was slightly greater in the White crania than in the Negro crania of the Hamann Museum. He likewise ascertained that this racial difference was consistent for the sexes. It is true that the difference was not very pronounced, being only 1·5 mm. in the case of the males, and exactly 1 mm. in the case of the females. In spite of this fact, the writer felt that it was worthy of being placed on record, more particularly in view of the fact that it obviously indicated a demand for an increase in the dimensions of the frontal segment of the cranial box, in order to provide accommodation for the evolutionary activity of the frontal lobes of the brain. It was therefore natural to assume that the lengthening of the pre-pituitary segment of the cranio-facial axis in the White races represented part of this scheme of evolutionary expansion.

RANGES OF VARIATION AND STANDARD DEVIATIONS OF THE POST-PITUITARY SEGMENT OF THE CRANIO-FACIAL AXIS IN THE HAMANN MUSEUM WHITE AND NEGRO CRANIA

These ranges were rather extensive, just as in the case of the pre-pituitary segment. The maximum for the male White crania was 59·0 mm., and the minimum 41·0 mm., the actual range being thus as much as 18 mm., which would be regarded as excessive. It was fractionally less in the case of the male Negroes, the maximum being 57·0 mm., and the minimum 39·5 mm. This racial difference was likewise shown by the female crania, the range being 9·5 mm. for the female White crania, and 8·5 mm. for the female Negro crania. It was thus significant to point out that the ranges of variation for both the pre-pituitary and the post-pituitary segments of the cranio-facial axis were consistently greater in the White than in the Negro crania. Indeed, the writer has been constantly impressed with the persistent way in which the ranges of variation of the measurements of the Hamann Museum White crania exceed those of the Negro crania in that Collection. Prof. Wingate Todd (10) has also emphasised this fact, and refers it to the remarkably heterogeneous character of the Hamann Museum White.

The standard deviations of the post-pituitary segment displayed some rather interesting results. In the first place it was noted that the racial difference was very slight, and, in the case of the female crania, practically negligible. Furthermore, it may be observed from Table II that the standard deviations were definitely higher in the males than in the females of both races,

thus suggesting the existence of a sexual factor. The coefficients of variability followed these results consistently.

Table II

The standard deviations and coefficients of variability of the post-pituitary segment of the cranio-facial axis are higher in the males than in the females for both the White and Negro crania of the Hamann Museum, thus suggesting the existence of a sexual factor.

	Standard deviations	Coefficients of variability
Male White	3·33 ±0·2051	6·86 ±0·4225
Female White	2·59 ±0·1595	5·75 ±0·3542
Male Negro	3·74 ±0·2303	7·71 ±0·4749
Female Negro	2·60 ±0·1601	5·65 ±0·3480

An investigation of the average dimensions of the post-pituitary segment disclosed the fact that there was very little racial difference. For example, the average for the male White crania was 48·7 mm., and for the male Negroes 48·6 mm., the difference in this case being negligible. It is true that the racial difference was more clearly demonstrated by the female crania, the average for the female Whites being 44·9 mm., as against 45·9 mm. for the female Negroes. This suggested of course the possible existence of a sexual factor, a fact which, however, would have to be confirmed by more extended researches.

There could certainly be no dubiety regarding the fact that in the Hamann Museum crania the length of the post-pituitary segment of the axis was more stable than that of the pre-pituitary segment. A few years ago the writer took advantage of this fact to formulate a new cranial index (3) which he termed the nasion-pituitary-basion index. In this the pre-pituitary segment was taken as representing 100, the index being therefore obtained by multiplying the post-pituitary segment by 100, and dividing the result by the pre-pituitary segment. It was found that this new index was consistent not only for race but also for sex. For example, the average index for the male White crania was ascertained to be 79·8. The interpretation of this was of course that the post-pituitary segment was, on the average, 79·8 per cent. of the pre-pituitary segment in this cranial group. On the other hand, the average index for the male Negro crania proved to be definitely higher, namely 81·6. These results, it may be added, were confirmed by the female crania, the average index for the female Whites being only 76·7, as contrasted with 79·8 for the female Negroes. It may therefore be noted that the index in each sex of the Hamann Museum White was definitely lower than the index for the corresponding sex of the Hamann Museum Negro, and likewise lower in the females than in the males of both races. The index thus informed us that the pre-pituitary segment was longer, relatively to the post-pituitary segment, in the Hamann Museum White than in the Hamann Museum Negro.

THE ANGLE OF CRANIAL FLEXION IN THE HAMANN MUSEUM WHITE AND NEGRO CRANIA

The writer has already explained that this is the angle formed by the pre-pituitary and post-pituitary segments of the cranio-facial axis. He has made a previous study (2) of this angle in the Hamann Museum White and

Negro crania, including a description of the method of measuring it. It is essential that he should again refer to its average size in these four cranial groups, as this will have an important bearing upon its comparative anatomy. In the first place he noted that its average size was less in the White than in the Negro crania. In the second place it was observed that it was, on the average, smaller in the males than in the females of both races. It was evident, therefore, that he had discovered a cranial angle which consistently exhibited not only racial but also sexual differences. For example, its average size in the male White crania was 131·3°, whereas in the male Negroes it was 135·1°. Furthermore, its average size in the female White crania was 133·7°, as compared with 136·7° in the female Negroes. It is likewise important to mention that the angle displayed very wide ranges of variation. For instance, one male Negro cranium (No. 662) possessed an angle of 162·5°, which was comparable to the dimensions found in the higher anthropoids (see Table III).

COMPARATIVE ANATOMY OF THE ANGLE OF CRANIAL FLEXION

Our observations on this angle in Man have demonstrated to us that it was larger on the average in the Negro than in the White. The natural assumption should therefore be that it would show a progressive increase as one descended the mammalian scale. The anthropoid that showed the closest approximation to the dimensions found in the Hominidae was the chimpanzee (B 240 of the Hamann Museum). This skull yielded an angle of 159°. The gorilla, which is regarded by some authorities as the most highly evolved member of the anthropoid group, yielded a rather surprising result. The only skull (B 170 of the Hamann Museum) that was available to represent this type possessed an angle of 178°, which, as it happened, was exactly the same figure as that for the more lowly evolved gibbon (B 549 of the Hamann Museum). It was therefore manifest that this angle must display in these lower Primates the usual wide ranges of variation that are found in Man. It is important to mention once more that only one mesially sectioned skull was available to represent each of the lower mammalian types in this research. It is thus obvious that a considerable time will have to elapse before a sufficient number of mesially sectioned crania is available for the purpose of estimating the average size of the angle in lower Mammals. The orang skull (B 551 of the Hamann Museum) yielded an angle of 161°, which was very nearly as small as that shown by the chimpanzee.

The skull of a macaque monkey (B 416 of the Hamann Museum) was available to represent the lower anthropoids. It possessed an angle of 173°, which was definitely larger than those found in the chimpanzee and orang, but slightly smaller than those displayed by the gorilla and gibbon skulls.

The skull of a lemur (B 197 of the Hamann Museum) presented an angle of 179°, the result being that in this specimen the pre-pituitary and post-pituitary

segments of the cranio-facial axis formed almost a straight line (see Plate V). It is thus clear that the evidence we have gleaned from a study of crania representing the anthropoid apes, the lower anthropoids and the lemurs, that the pre-pituitary and post-pituitary segments become gradually opened out like the leaves of a hinge. To carry the analogy a little further, one may note that in this lemur skull the two leaves were almost straight apart, thus practically obliterating the angle of cranial flexion.

The greatest surprise of this investigation was that afforded by the skull of *Tarsius* (B 135 of the Hamann Museum). This specimen was of course so small that it had to be studied by means of a binocular loupe. The writer was candidly astonished to find that it possessed a well-marked degree of cranial flexion (see Plate IV). The angle registered 151°, which was definitely less than that displayed by any of the higher anthropoid crania studied in this research. It was thus remarkable to note that this genus could exhibit a degree of cranial flexion 28° less than that shown by another member of the Lemuroidea, namely *Lemur catta*. This discovery, it may be added, was of importance as a contribution to the discussions that have been conducted by Wood Jones and other writers regarding the position of *Tarsius* in the evolutionary scale. The writer has no intention of entering further into these discussions, as the length of this paper would thereby be unduly prolonged.

The next mammalian type that was studied, namely the dog, which was selected to represent the important Carnivora group, showed an amazing transformation of the cranio-facial axis. The writer has just been comparing the two segments of the axis with the two leaves of a hinge, and pointed out that in the lemur skull these had opened out so as to form almost a straight line. The skull of a dog (see Plate V) displayed a much more advanced stage of this opening-out process, the result being that the angle of cranial flexion now registered far more than two right angles, the actual measurement being 208°. The skull of another dog, which was available to the writer, displayed an angle of 198°. This provided us with further information regarding the fact that this angle exhibited wide ranges of variation in these lower mammalian forms, just as in Man. An inspection of Plate V will show that the salient of the angle, instead of being directed upwards as in the higher mammalian forms, was now directed downwards. It is obvious that in effecting this transformation both the pre-pituitary and the post-pituitary segments of the cranio-facial axis must have been implicated. The discussion of these features will be found in the next two sections of this paper.

Table III has been designed to show at a glance the comparative anatomy of the angle of cranial flexion. The first point to notice is, that a vast evolutionary gap exists between the anthropoids and Man, and also between the Primates and the lower Mammalia. Thus the average size of the angle in the male Negro is 24° less than in the nearest anthropoid, namely the chimpanzee. In the next place, it is important to direct attention once more to the marked degree of cranial flexion exhibited by the skull of *Tarsius*.

Table III

There is a gradual and progressive increase in the size of the angle of cranial flexion as one descends the mammalian scale. Note the vast evolutionary gap between the Hominidae and the anthropoid apes.

Hamann Museum male White ...	131·3°
Hamann Museum male Negro ...	135·1°
Evolutionary gap	
Chimpanzee	159·0°
Orang	161·0°
Gorilla	178·0°
Gibbon	178·0°
Macaque	173·0°
Tarsius	151·0°
Lemur	179·0°
Evolutionary gap	
Dog	208·0°

THE ANGLE OF INCLINATION OF THE PRE-PITUITARY SEGMENT OF THE CRANIO-FACIAL AXIS TO THE FRANKFORT PLANE

The writer recently made a preliminary communication (5) on this subject, founded upon observations made on the Hamann Museum White and Negro crania. In another paper (8) he explained the method of estimating the size of this angle. Since that time he has been privileged to investigate this matter in representative types of Primates and lower Mammals. In the case of the human crania he found that the pre-pituitary segment made a relatively small angle with the Frankfort plane, which did not appear to display any definite racial differences. Thus the average size of the angle in the male Whites was 7·1°, as compared with 5·5° for the male Negroes. On the other hand, it registered 5·9° in the female Whites and 6·1° in the female Negroes. That is to say, it was slightly larger in the male Whites than in the male Negroes, but smaller in the female Whites than in the female Negroes. An investigation of the comparative anatomy of the angle disclosed the fact that it became rapidly larger as one descended the mammalian scale. Thus the anthropoid that possessed the dimension most closely approximating to that found in Man was the chimpanzee. Yet in this skull the angle was as much as 15·5°, that is to say, more than twice the average found in the Hominidae. The skull of an orang came next, with 18·5°. The gibbon skull, as was to be expected from its more lowly evolved organisation, displayed an angle of 22°. The gorilla skull occupied a most anomalous position, for it yielded an angle much larger than that of the gibbon, namely 28·5°. One would thus suspect that the angle must possess wide ranges of variation in these lower Primates, just as in Man. The skull of a macaque monkey, which was again selected to represent the lower anthropoids, possessed an angle of 25°. The lemur skull, as was to be expected, exhibited an angle slightly larger, namely 26·5°. The *Tarsius* skull, however, claimed once more a favourable position in the evolutionary scale by displaying an angle of only 22°, the same as that shown by the gibbon skull. The skull of the dog displayed a marked increase in the size of the angle, which registered 34·5°. As the position of the Frankfort plane is indicated

by the white lines in all the plates illustrating this paper, the gradual increase in the degree of inclination of the pre-pituitary segment to that plane can be readily studied as one descends the mammalian phylum.

Table IV

The angle of inclination of the pre-pituitary segment of the cranio-facial axis to the Frankfort plane exhibits a marked increase as one descends the mammalian scale. Note the evolutionary gap between Man and the higher anthropoids.

Hamann Museum male White ...	7·1°
Evolutionary gap	
Chimpanzee	15·5°
Orang	18·5°
Gibbon	22·0°
Gorilla	28·5°
Macaque	25·0°
Tarsius	22·0°
Lemur	26·5°
Dog	34·5°

The writer feels in duty bound to offer some suggestions regarding this very pronounced displacement upwards of the pre-pituitary segment of the cranio-facial axis in lower mammalian forms. A study of the skull of the dog in Plate V certainly suggests that the nasion has become deliberately forced upwards by some means or other. As the latter point represents the junction of the maxillary portion of the skull with the cranial portion, it is evident that this upward movement of the nasion is part of the scheme whereby the jaws gradually dominate the cranial portion of the skull more and more as one descends the mammalian scale. The writer regrets that space does not permit a fuller discussion of this most interesting topic.

THE ANGLE OF INCLINATION OF THE POST-PITUITARY SEGMENT OF THE CRANIO-FACIAL AXIS TO THE FRANKFORT PLANE

The writer has recently been able to make a preliminary announcement(5) on this subject, including a description of the method of measuring this angle. Since then, he has been enabled to make a further study of this question in lower mammalian types. He found that in the case of the human crania the average size of the angle formed between the post-pituitary segment of the cranio-facial axis and the Frankfort plane displayed very remarkable racial and sexual consistency. Thus he found that the average size of this angle in the Hamann Museum male White crania was 122·8°, while in the Hamann Museum male Negroes it was definitely greater, namely 129·5°. That is to say, the angle showed a tendency to increase in the lower racial type. As a matter of fact, in one male Negro skull the angle registered 144·5°, and in one female Negro skull 152·5°, dimensions which were as great as those exhibited by some of the anthropoid crania (see Table V). This racial difference was likewise displayed by the female crania. For instance, the average size of the angle in the female White crania proved to be 127·2°, whereas in the female Negroes it was again greater, namely 131·3°. It may also be noted that there was

a sexual factor, as well as a racial factor, that determined the size of the angle. Thus the average dimension in the female White crania was 127·2°, and only 122·8° in the males, thus yielding a sexual difference of 4·4°. Furthermore, this sexual difference was likewise displayed by the Negro crania, for it may be observed that the average size of the angle in the males was 129·5°, whereas in the females it was again larger, namely 131·3°.

There could thus be no reasonable doubt regarding the fact that the post-pituitary segment of the cranio-facial axis exhibited a closer approximation to the horizontal in the Hamann Museum Negro than in the Hamann Museum White. Therefore the natural assumption should be that this approximation towards 180° would become more and more pronounced as one descended the mammalian scale. On further study this premise was ascertained to be correct. The orang was the anthropoid ape that showed the closest approach to Man, with an angle of 145·5°. In the chimpanzee it was 147°, in the gorilla 149° and in the gibbon 146·5°. In the skull of a macaque monkey the angle registered 147°. It may thus be noted that there was a very wide evolutionary gap between Man and the highest anthropoids (see Table V).

The skull of *Tarsius* again provided a most interesting study, for in it the angle of inclination was as low as 130°. That is to say, it was comparable to the average dimensions of the angle as found in Man. The size of the angle found in *Tarsius* was in striking contrast to the large dimension of 155°, which was yielded by the skull of *Lemur catta*. The skull of the dog provided an angle of 175·5°, which meant of course that in this specimen the post-pituitary segment of the cranio-facial axis was very nearly parallel to the Frankfort plane (see Plate V).

Table V

The angle of inclination of the post-pituitary segment of the cranio-facial axis to the Frankfort plane exhibits a gradual approximation to 180° as one descends the mammalian scale. Note the marked evolutionary gap between Man and the higher anthropoids.

Hamann Museum male White ...	122·8°
Hamann Museum male Negro ...	129·5°
Evolutionary gap	
Orang	145·5°
Gibbon	146·5°
Chimpanzee	147·0°
Gorilla	149·0°
Macaque	147·0°
Tarsius	130·0°
Lemur	155·0°
Dog	175·5°

THE OLFACTORY POCKET

This is the term which has been adopted by the writer for the portion of the cranial cavity which becomes cut off by the pre-pituitary segment of the cranio-facial axis. A study of the skull of the dog in Plate V shows that a considerable portion of the cranial cavity becomes thus mapped off in this particular specimen. The term "olfactory pocket" may not be altogether a

happy one, but there can be no doubt regarding the fact that it must possess an intimate relationship to the olfactory portion of the brain. For instance, in the skull of the dog displayed in Plate V it may be noted that the pocket is floored to a considerable extent by the cribriform plate of the ethmoid, which shows very clearly the perforations for the olfactory nerves. In all the photographs that illustrate this memoir the pocket has been indicated by dotted lines, so as to make its delineation more clear. It will be observed that the pocket tends to become obliterated as one ascends the mammalian scale. The writer was much struck by the fact that it was practically absent in the lemur skull, as Plate V shows. In the skull of *Tarsius* (Plate IV) the pocket formed a tiny recess under the anterior extremity of the cranio-facial axis. In the skull of the macaque monkey (Plate III) the pocket will be observed to be narrow, but relatively deep.

In the crania of the higher anthropoids the olfactory pocket was found to display great variations in size. It was smallest in the chimpanzee skull and largest in the gorilla skull, but it was likewise well marked in the orang and gibbon skulls.

The writer has so far been unable to make an extensive study of the relative proportions of the olfactory pocket in the Hominidae. However, his preliminary observations show that it is as a rule non-existent in the crania of the white races. That is to say, in these racial types the pre-pituitary segment of the cranio-facial axis is usually below the level of the cribriform plate of the ethmoid. In the Negro skull illustrating this memoir there was a definite olfactory pocket, as shown in Plate I. The question of its relative frequency and the study of its comparative dimensions in Man will, however, have to be postponed to a future date.

CONCLUSIONS

1. The cranio-facial axis devised by the author consists of a pre-pituitary and a post-pituitary segment. He was privileged to study in the Hamann Museum its comparative anatomy in representative types of anthropoids and lower Mammals, including a rare and unique genus such as *Tarsius*. The latter was found to exhibit an evolutionary phase of the cranio-facial axis in advance of that shown by the lemur and by many of the anthropoids.

2. This research on the cranio-facial axis divided itself very naturally into three phases:

   (*a*) The relative proportions of the two segments of the axis.
   (*b*) A study of the angle formed by these two segments.
   (*c*) The angle of inclination of each of these two segments to the Frankfort plane.

3. The writer has previously shown that a study of the relative proportions of the two segments of the axis in the Hamann Museum White and Negro crania provided a new cranial index which he termed the nasion-pituitary-

basion index. This index was found to exhibit remarkable racial and sexual consistency.

4. The angle formed by the two segments of the axis was termed by the writer the angle of cranial flexion. It displays a gradual increase in size as one descends the mammalian scale.

5. The angle of inclination of the pre-pituitary segment of the axis to the Frankfort plane exhibits a gradual increase in size as one descends the mammalian scale.

6. The degree of inclination of the post-pituitary segment to the Frankfort plane in Man was found to be controlled by two factors, racial and sexual. Thus the degree of inclination was less in the Hamann Museum White than in the Hamann Museum Negro, and also less in the males than in the females of both races. It exhibited a tendency to approximate to 180° as one descended the mammalian phylum.

7. The "olfactory pocket" is the term which has been adopted by the author for the portion of the cranial cavity which becomes cut off by the pre-pituitary segment of the cranio-facial axis. It tends to become obliterated as one ascends the mammalian scale.

DESCRIPTION OF PLATES I–V

Plate I

Fig. 1. Mesial section of Hamann Museum male White skull No. 696. This exhibits a marked degree of flexion of the cranio-facial axis. The olfactory pocket is absent in this skull. The Frankfort plane is indicated in this and the succeeding plates by white lines.

Fig. 2. Mesial section of Hamann Museum male Negro skull No. 662. In this specimen the angle of cranial flexion approximates to 180°. The olfactory pocket is represented by the dotted line, and is well marked.

Plate II

Fig. 1. Mesial section of chimpanzee skull B 240 in the Hamann Museum. Two-thirds natural size. The cranio-facial axis exhibits more flexion than in the gorilla skull, and the olfactory pocket is much smaller.

Fig. 2. Mesial section of gorilla skull B 170 in the Hamann Museum. One-half natural size. The cranio-facial axis forms almost a straight line. The olfactory pocket is well marked.

Plate III

Fig. 1. Mesial section of orang skull B 551 in the Hamann Museum. Two-thirds natural size. The angle of cranial flexion is approximating to 180°. The olfactory pocket is well marked.

Fig. 2. Mesial section of the skull of a macaque monkey (B 416 of the Hamann Museum). Natural size. The two segments of the cranio-facial axis are very nearly in line. The olfactory pocket is narrow but relatively deep.

Plate IV

Fig. 1. Mesial section of gibbon skull B 549 in the Hamann Museum. One and one-third times the natural size. The two segments of the cranio-facial axis are almost in line. The olfactory pocket is well defined.

Fig. 2. Mesial section of the skull of *Tarsius* (B 135 of the Hamann Museum). Two and a half times the natural size. The cranio-facial axis exhibits as much flexion as in the higher anthropoids. The olfactory pocket is very small.

PLATE V

Fig. 1. Mesial section of the skull of a dog (B 128 of the Hamann Museum). One-half natural size. The cranio-facial axis has become profoundly altered, the angle of cranial flexion now forming a salient downwards. The olfactory pocket is very extensive and is floored to a considerable extent by the cribriform plate of the ethmoid.

Fig. 2. Mesial section of the skull of a lemur (B 197 of the Hamann Museum). Natural size. The two segments of the cranio-facial axis form practically a straight line. This specimen exhibits no olfactory pocket.

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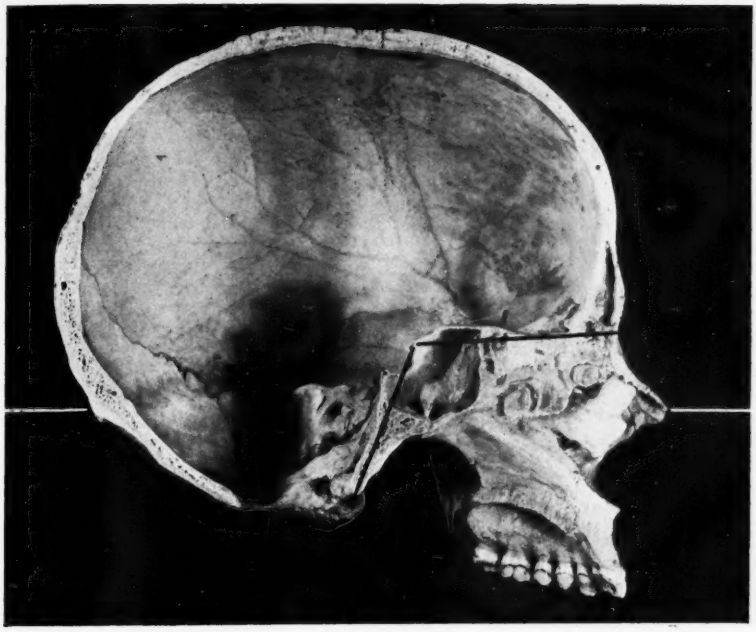

Fig. 1. Male White skull

Fig. 2. Male Negro skull

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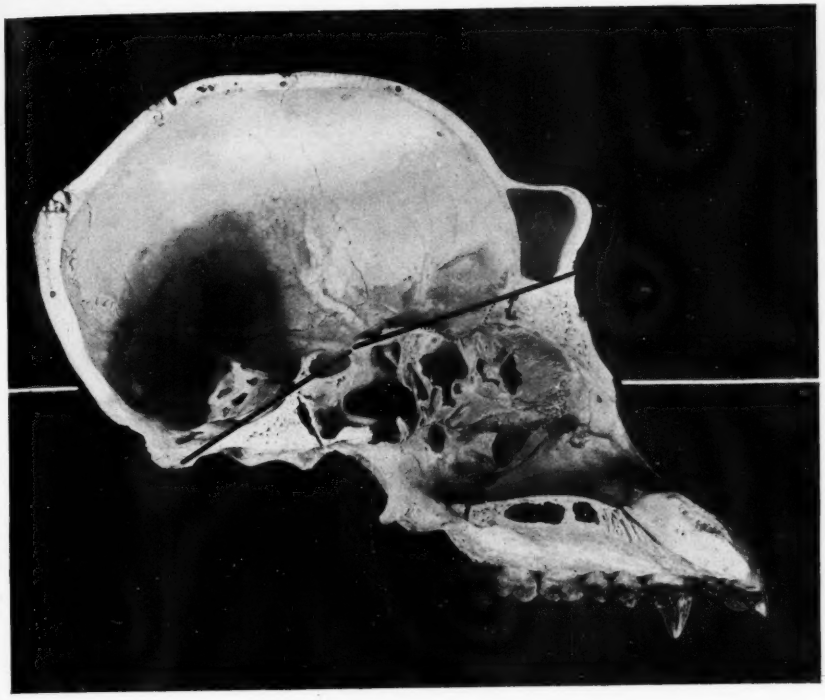

Fig. 1. Chimpanzee skull

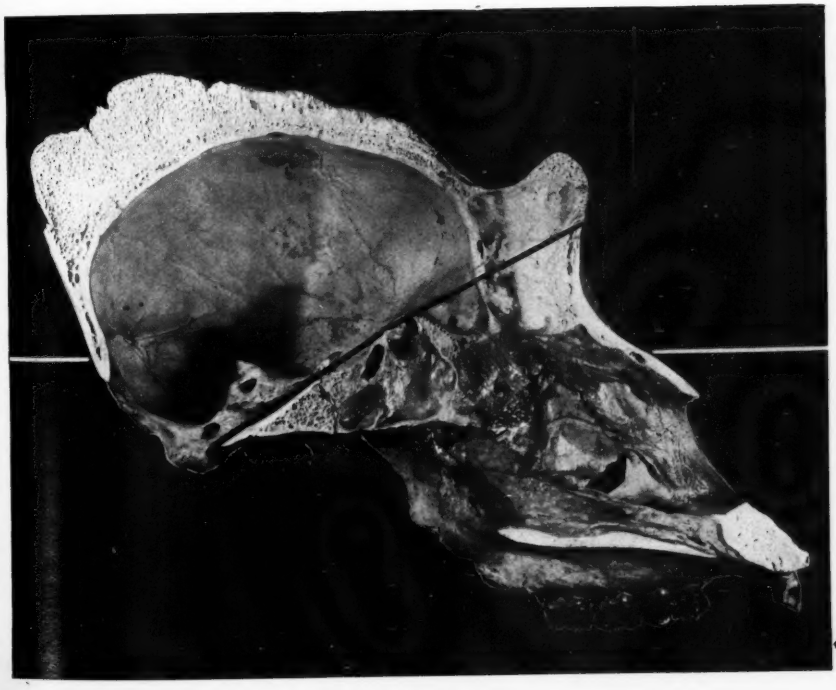

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Fig. 2. Gorilla skull

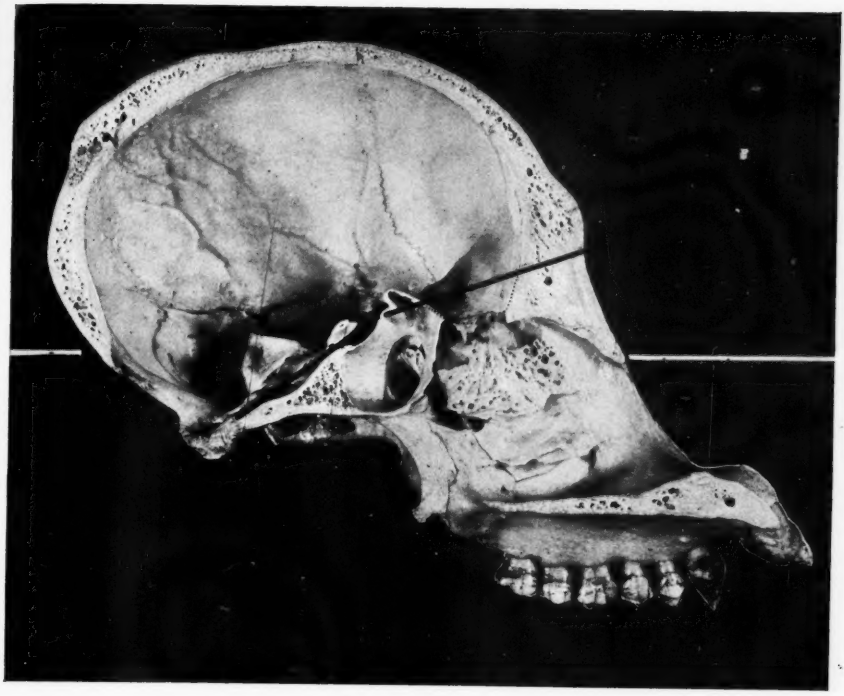

Fig. 1. Orang skull

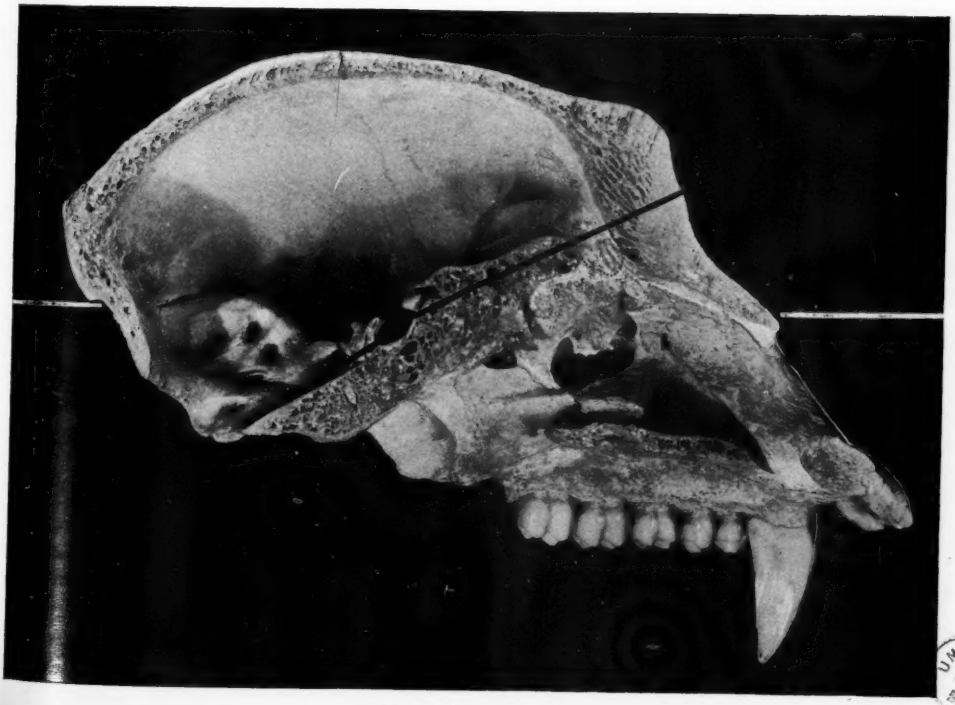

Fig. 2. Macaque skull

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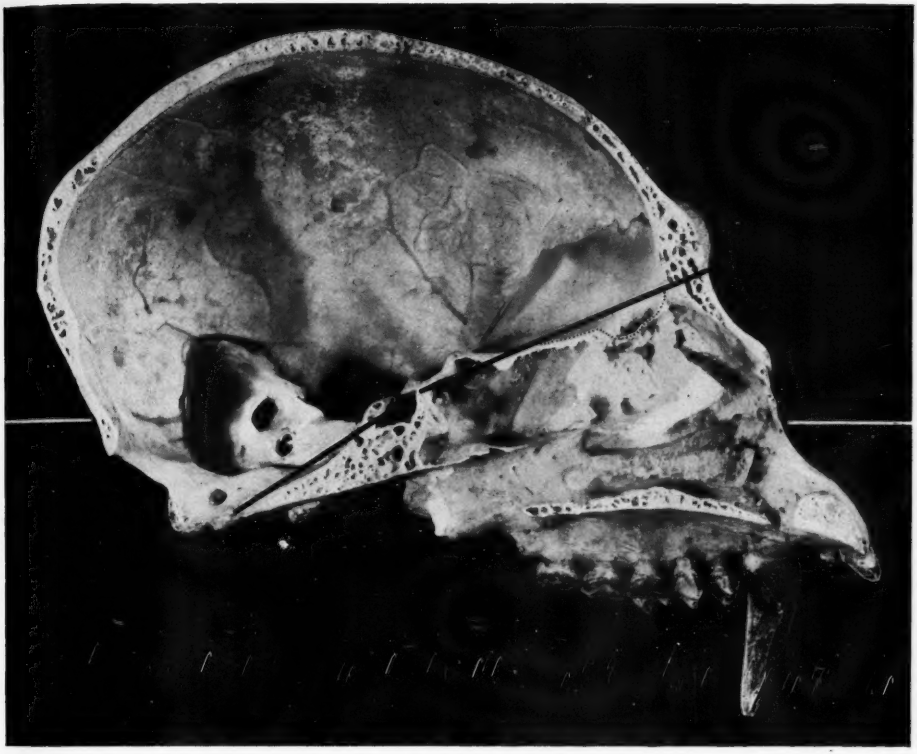

Fig. 1. Gibbon skull

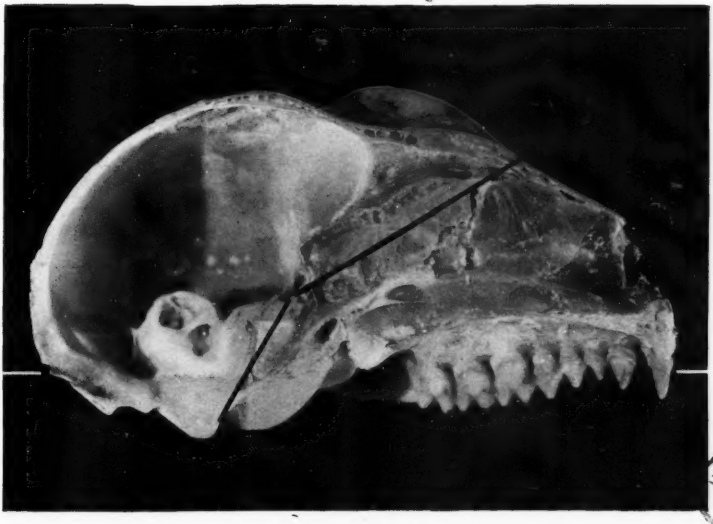

Fig. 2. Tarsius skull

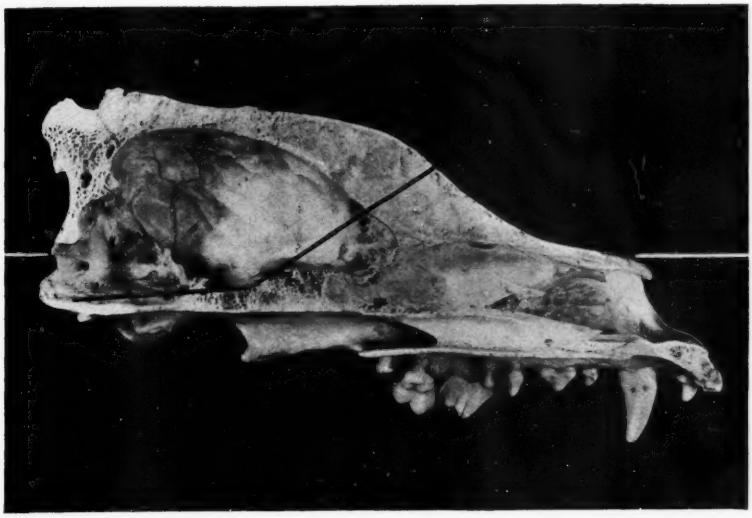

Fig. 1. Dog skull

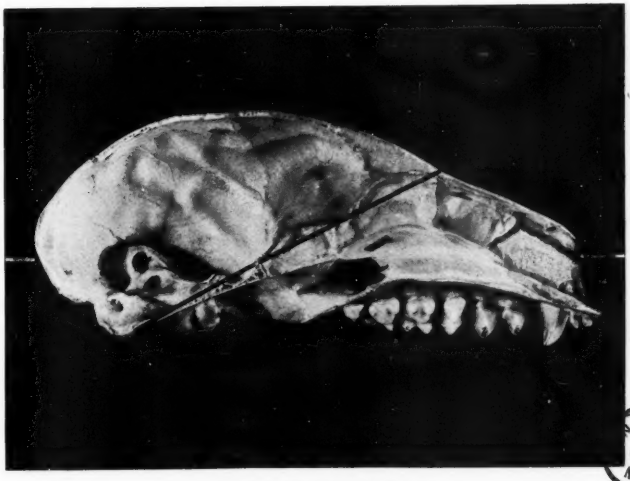

Fig. 2. Lemur skull

ON FUSION OF THE ATLAS AND AXIS VERTEBRAE

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INTRODUCTORY

The condition of true, non-pathological fusion of the atlas and axis vertebrae constitutes an extremely rare anomaly—perhaps the rarest of all the many and varied manifestations of irregular segmentation affecting the vertebral axis. But few cases occur in the whole of the literature, a fact which is not very surprising when one considers the functional importance of the atlanto-axial articulation, and the disability necessarily consequent upon any grave developmental disturbance of that mechanism. Additional examples may have been overlooked in the past, since the older anatomists (e.g. Macalister (1)) dismissed all such fusions as entirely the result of pathological change; and although Dwight (2) had in 1901 figured and briefly mentioned an undoubted specimen of complete atlanto-axial fusion, it was not until Elliot Smith (3) in 1907–9 described what must be regarded as the classical case that the correct nature and interpretation of this most interesting vertebral variation was finally established.

In this paper attention is drawn, without apology, to further, if somewhat incomplete, cases.

TYPES OF ATLANTO-AXIAL FUSION

If merely descriptive terminology be employed, the following classification covers all known cases of fusion of the first pair of cervical vertebrae:

Group 1. Fusion of the separated odontoid process with the ventral atlantal arch.

Group 2. Complete (= bilateral) fusion of atlas and axis with or without attempted assimilation of the first vertebra by the second.

Group 3. Incomplete (= unilateral) fusion, one-half of the atlas retaining its independence, with or without some degree of assimilation.

Morphologically speaking, cases in Group 1 are purely atlantal in nature: the atlas centrum is restored to its proper vertebra and may be further separated from the axis centrum by the interposition of a genuine fibro-cartilage. A number of such cases have been recorded. Thus, Le Double (4), though not quoting any personal case, makes mention of three specimens—one in the Siena Museum, one (No. 9966) of Dwight's collecting in the Warren Museum of Harvard Medical School, and, in the same museum, a plaster cast of another specimen of French origin. In 1924 Hunter (5) reported an excellent example,

referring in his paper to a further case in the private collection of Prof. Bolk, showing occipito-atlantal synostosis in addition to the odonto-atlantal fusion.

Group 2 contains the famous cases of Dwight and Elliot Smith, to which a third may here be added from the Hunterian Museum of the Royal College of Surgeons.

Dwight's case (spine *H* 3 in his account) constitutes Group C of Class IV in that author's classification of the anomalous spines in the Warren Museum of the Harvard Medical School. The specimen, from an old insane woman, has the vertebral formula C. 6, Th. 12, L. 6, S. 6, Cocc. 4, "as if the thorax had moved a step upward." Of the six cervical vertebrae, the atlas and axis are indistinguishably fused: the odontoid apex is recognisable; the atlantal posterior arch is well developed and the superior atlantal articular processes are "nearly plane." The VIth cervical vertebra has the characters of a normal VIIth, and the VIIth itself those of the normal Ist thoracic; the last (VIth) lumbar vertebra is sacralised on the left side. Elliot Smith's case was taken from an adult Ancient Egyptian, whose spinal column exhibited a remarkably consistent series of segmental errors, best summarised by Bateson's(6) term *backward homoeosis*, for this spine presented the following features: manifestation of an occipital vertebra; fusion of atlas with axis; a right cervical rib on the VIIth cervical vertebra; the assumption of lumbar characters by the XIIth thoracic vertebra; the assumption of Vth lumbar characters by the IVth lumbar vertebra, and fusion of the real Vth lumbar vertebra with the sacrum.

The atlas and axis, originally separate, were united by ossification of the capsular and anterior atlanto-axial ligaments: the right half of the transverse ligament was ossified and ankylosed to the back of the odontoid process, to the front of which the atlantal anterior arch was further fused: the left half of the first neural arch remained independent both of the axis and of its fellow, this last being much depressed and assimilated by the axial arch below.

To permit of rotary movements of the cranium, the upper atlantal processes had been modified into flat and sloping articular surfaces, i.e. had assumed definitely axial features.

The Hunterian Museum specimen is No. 503, Teratological Series, comprising an adult anomalous cervical spine of only six vertebrae. The atlas and axis are completely fused, the composite piece bearing but one transverse process on the right, and two on the left. The IVth and VIth cervical vertebrae manifest laminar irregularities; the Vth has the characters of a normal VIIth, whilst the VIth also departs markedly from type. There is nothing further known about the vertebral formula, the neck only being preserved.

It is likely that a survey of further teratological material in anatomical museums throughout the country would reveal additional examples of atlanto-axial concrescence, as might also a careful and critical examination of clinical cases of Willet-Sprengel shoulder, brevicollis, and the like, wherein the cervical spine is invariably of anomalous constitution.

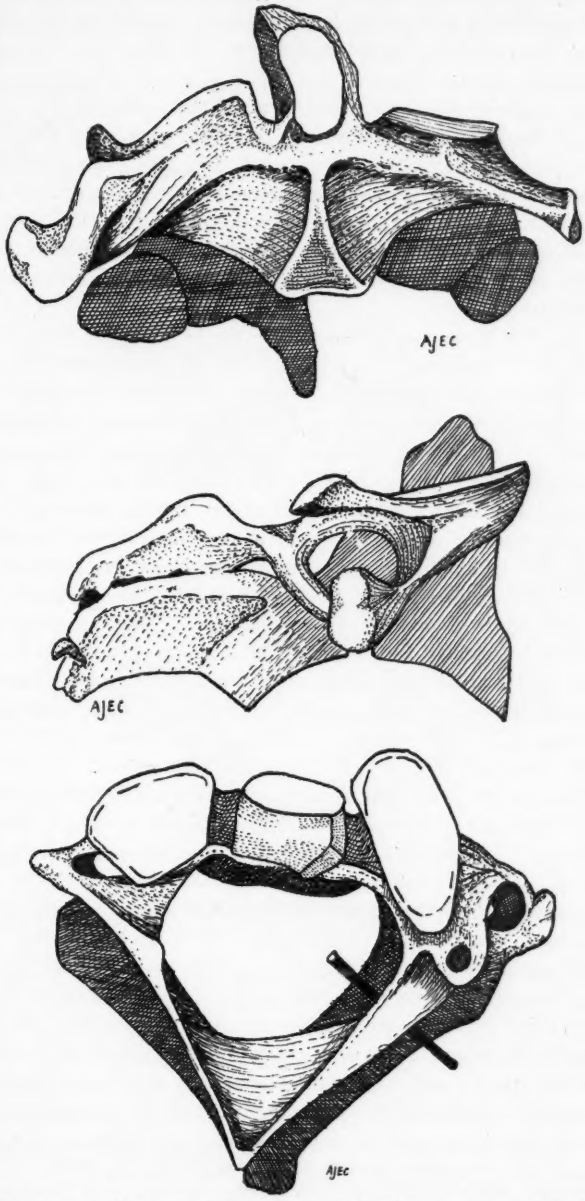

Fig. 1. Specimen *A* (University College, London). Anterior, superior and right lateral aspects of fused (half) atlas and axis.

Recently, Tramontano-Guerritore(7) has mentioned the condition of atlanto-axial synostosis with some familiarity, in connection with metameric variation in the occipito-atlantal region, but his paper does not detail any specific instance.

Group 3 contains the two cases herein briefly described: Specimen *A* (probably of Prof. Thane's collecting) from the Anatomy Department of University College, London, and specimen *B* from the Anatomical Museum of Birmingham University. Neither specimen has any history, the condition and constitution of the spinal column being unknown in both. These two specimens are the sole manifestations of atlanto-axial synostosis encountered during the past few years in a comprehensive study of anomalous cervical material from many sources[1].

Specimen *A* is a composite bony piece made up of an entire adult axis vertebra together with the very intimately incorporated right half or so of its cephalic neighbour, whose left half, present during life, is lacking (see fig. 1). The sturdy odontoid process, bearing a large atlantal facet, is deflected to the right; the left half of the conjoined piece is entirely axial in nature, as evidenced by the characters of the upper and lower articular, and of the transverse, processes. On the right, in the region of the lateral masses, the superior articular process is definitely of atlantal type (though greatly modified), the inferior, of axial type; the bony tissue between these two processes, scarcely thicker (deeper) than the purely axial left portion of the specimen, nevertheless represents both atlas and axis mingled in a fusion so complete and so intimate as to justify the description "assimilation of the atlas by the axis." The large single transverse process, representing the fused processes of the two vertebrae, is atlantal in character; there is not the slightest indication of the dual nature of this process any more than that of the fused lateral masses (see fig. 1). Immediately behind the transverse process an intervertebral foramen gives exit to the second spinal nerve: behind the foramen the atlantal neural arch fuses with the corresponding subjacent structure, though to no severe degree. The atlantal component of the composite arch is readily detectable right back to the middle line where it blends with the left half of the axial neural arch, in the same plane as which it lies throughout its course. In consequence, the subjacent right axial neural arch carrying with it the corresponding half of the spinous process is, despite the synostosis, displaced downwards to a plane much below that of its fellow. An anterior atlantal arch is wanting, being probably part of the absent left portion of the bone. The upper atlantal articular facet is spread out to cover the whole of the articular process, which has extended both antero-medially and postero-laterally. This upper facet is markedly flattened, retaining but faintly its general concavity,

[1] Namely, the Hunterian Museum, Royal College of Surgeons; University College and King's College, London; the Universities of Leeds, Manchester, Birmingham, Sheffield, and Liverpool; University College, Cardiff, and Trinity College, Dublin. I sincerely thank the respective heads of these several Anatomy Departments for their great courtesy in permitting me access to material in their care.

and then mainly in its hinder portion. Rotary movements must certainly have occurred, and with considerable facility, at the right occipito-atlantal articulation.

Specimen *B* (see fig. 2) consists of a complete adult axis vertebra with which is fused the right half of the corresponding atlas, the left moiety of which, undoubtedly present during life, is now lost. The second vertebra is slightly asymmetrical; its right superior articular process is invisible owing to the

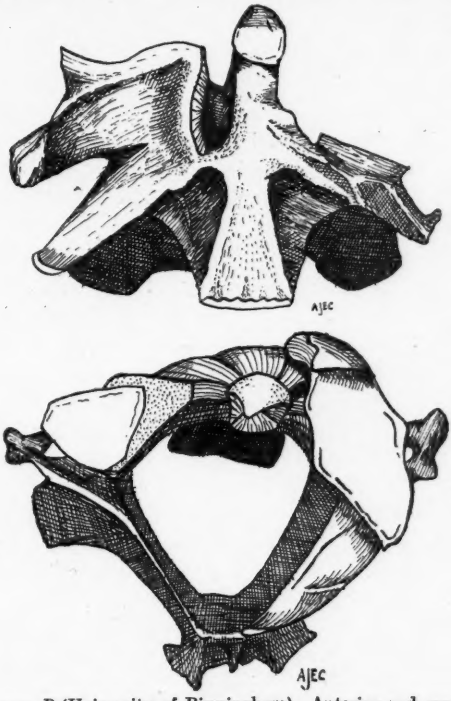

Fig. 2. Specimen *B* (University of Birmingham). Anterior and superior aspects of fused (half) atlas and axis.

fusion, and its spine is atypical, being composed of a tiny median bony spicule flanked on either side by a larger, very irregularly tuberculated prominence. The odontoid process is deflected markedly backwards and to the left, so that its atlantal facet, borne high on its summit, looks upwards rather than forwards and, lying altogether above the level of the ventral atlantal arch, may very well have articulated with the occipital bone: its neck is grooved for the transverse ligament, which apparently existed with more or less its customary connections. Both laminae bear a pronounced groove for the second spinal nerve.

Of the atlas, only the right lateral mass and corresponding half of the

neural arch are present: the former is perfectly continuous with the axis below (a faint lateral groove and a couple of vascular foramina alone giving any hint of previous independent existence), whilst its superior articular process juts out considerably in advance of the axial body, ending abruptly in a sharply recurved lip. There is no trace of anterior arch, the odontoid neck presenting bony continuity with the anterior recurved extremity of the lateral mass.

The (upper) atlantal articular surface has undergone definite modification; whilst generally faintly concave in its long axis and also anteriorly in its transverse axis, yet in its hinder portion it is distinctly convex, tending to assume the characters of the articular shoulders of the axis, and strongly indicative of an attempt at the provision for rotary movement at the occipito-atlantal articulation. That such movement was indeed performed, and especially in the left-to-right direction, is further evidenced by a backward prolongation of the superior atlantal facet and by the impress made by the (now missing) left inferior atlantal process upon the left side of the base of the odontoid process (stippled area in fig. 2).

The right atlantal transverse process is well formed and typical; the right half of the neural arch, deeply grooved by the vertebral artery, runs clear of, though extremely close to, the subjacent arch, terminating posteriorly in unattached fashion.

COMMENTARY

The two cases described are necessarily incomplete for want of information concerning the constitution of the remainder of the vertebral column and the condition of the margins of the foramen magnum. They are advanced, however, in the hope that search for further examples may be induced, and our knowledge of this particular variation may thereby be augmented.

The synostosis involves the identical atlantal portion in both cases, but to a much greater degree in case *A* than in case *B*. In the former (undoubtedly congenital in nature) the features of the lateral mass region and of the compound transverse process indicate the occurrence of the anomaly at a date much preceding the time of fusion in case *B*.

It is difficult to determine with certainty whether atlas and axis enjoyed previous independence, undergoing subsequent fusion, or whether an original atlanto-axial segmental cleavage failed to occur. The available evidence, particularly that offered by the presence of the second spinal nerve, is in favour of an intimate fusion of two originally separate elements.

In specimen *B* the first two cervical vertebrae have formed independently, and have suffered fusion either late in development or (as is likely enough) early in post-natal life. Were the absent atlantal moiety restored, this case would resemble those of Dwight and Elliot Smith in the possession of distinct atlantal and axial transverse processes bilaterally.

In both *A* and *B* a *ligamentum transversum atlantis* was present and provision made (cf. Elliot Smith's case) for rotation of the cranium by com-

pensatory modifications of the right occipito-atlantal—and also in case *B* of the left atlanto-axial—articulations.

No more excellent demonstration could be afforded of the body's potential resources for successfully combating a serious initial handicap or for the bold modification of structure in the maintenance of essential function.

I wish to express my indebtedness to Sir Arthur Keith for information regarding the Hunterian specimen (No. 503, Terat. Ser.), to Prof. G. Elliot Smith, F.R.S., and to Prof. J. C. Brash for generous permission both to examine and to describe the two most interesting specimens which form the main subject-matter of this paper.

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A REPORT ON A SPECIMEN OF FUSED PELVIC KIDNEY FOUND IN A BANTU NATIVE OF SOUTH AFRICA

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University of the Witwatersrand, Johannesburg

THE case recorded in this paper is, it is thought, sufficiently uncommon to justify publication, and, perhaps, to interest the anatomist, urologist and others.

For the specimen, which is preserved in the Anatomy Museum of the University of the Witwatersrand, I am indebted to Dr A. Sutherland Strachan, pathologist to the South African Institute for Medical Research, Johannesburg.

The renal organs exhibit the anomalous conditions of multiplicity, fusion and ectopia, being situated in the pelvis.

The specimen was found in the routine post-mortem examination of a male Zulu aged 30. The post-mortem findings included oedema of the lungs and ascites, due to heart failure and arteri-osclerosis. There had been no abnormality of the kidney functions other than albuminuria and some diminution of urinary output during the few days of fever that preceded death. Evidently the cause of death lay in circumstances unconnected with the ectopia and other abnormalities of the renal organs. As the presence of abnormality was quite unsuspected, it is a matter for congratulation that the specimen was so little damaged. Evidently care had been taken to minimise the inevitable damage.

The whole mass of pelvic viscera with peritoneum had been removed; the bladder had been opened in the mid-ventral line and incisions had been made into the kidney after the manner of post-mortem routine. On receipt at the laboratory an attempt was made to restore the organs to a natural position before hardening by careful suture of the organs and of the peritoneum and by packing with pledgets of cotton-wool. The specimen was immersed in 5 per cent. formalin solution for three weeks prior to dissection.

POSITION

In general terms, the fused renal organs constitute a thick discoidal mass which covers the promontory of the sacrum. Fig. 1 is a pen and ink drawing from a photograph of the posterior aspect of the renal organ with adnexa taken after reconstruction and dissection. The posterior surface bears a deep impression which evidently corresponds to the promontory of the sacrum. This impression measures 4·8 cm. across and is 6·3 cm. from the lowest point of the kidney.

It was found that 5·2 cm. was an average measurement across the promontory of the male Zulu sacrum and 10·9 cm. an average mid-line length.

If it be assumed that the length of the sacrum corresponding to this specimen maintained these same proportions it may be inferred that the sacrum was 10 cm. in length (i.e. 10·9 reduced in the proportion 5·2 to 4·8). It is then concluded that the lowest point of the kidney was probably 3·7 cm. or $1\frac{7}{16}$ in. above the lowest point of the sacrum.

The distal portions of the two common iliac arteries, cut from the aorta, are adherent to the upper and lateral borders of the renal organ. It seems certain from examination and measurements that the common iliac arteries

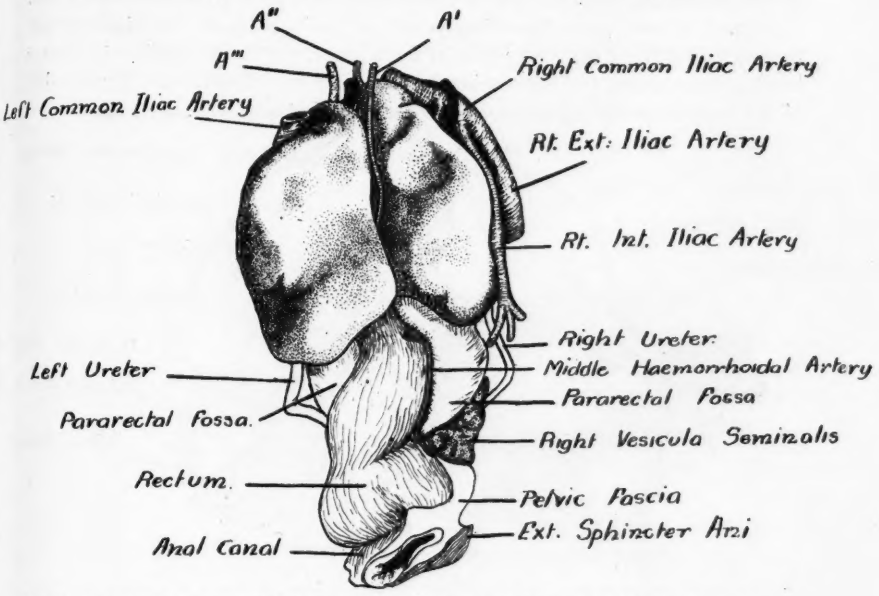

Fig. 1. This figure is a reproduction in pen and ink of a photograph of the fused renal organs dissected from the posterior aspect. Explanatory annotations of the more prominent structures are given.

must have been cut very close to their origins from the aorta, that is to say, the renal organ in life had been very closely adapted to the bifurcation of the aorta.

The supra-renal glands, Dr Strachan informs me, occupied a normal abdominal position.

DISSECTION

The general appearance of the dissected specimen is shown from the posterior aspect in fig. 1, and from the right side in fig. 2 which is also drawn from a photograph.

The whole organ is roughly bisected in the sagittal axis by a groove which

deepens to a cleft above and below. The upper cleft is shallow, but the lower is 5 cm. long and separates the two lower poles. The fusion of the kidneys is evidently, in the main, between the upper poles.

The rectum appears in the lower cleft, approximately median in position but rather more closely applied to the left lobe. The lower pole of the left lobe corresponds to the middle of Houston's three valves of the rectum, of which two lie on the right and one on the left side in this specimen.

A portion of the external sphincter ani muscle is preserved and is separated by 6·6 cm. (2⅝ in.) from the lowest point of the kidney in the dissected specimen.

Fig. 2 shows the recto-vesical pouch of peritoneum to the right of the rectum below the right lower pole of the kidney. In front of this, at a lower level, are the ureter and the seminal vesicle with the vas deferens. By the side of the rectum the middle haemorrhoidal artery is to be seen.

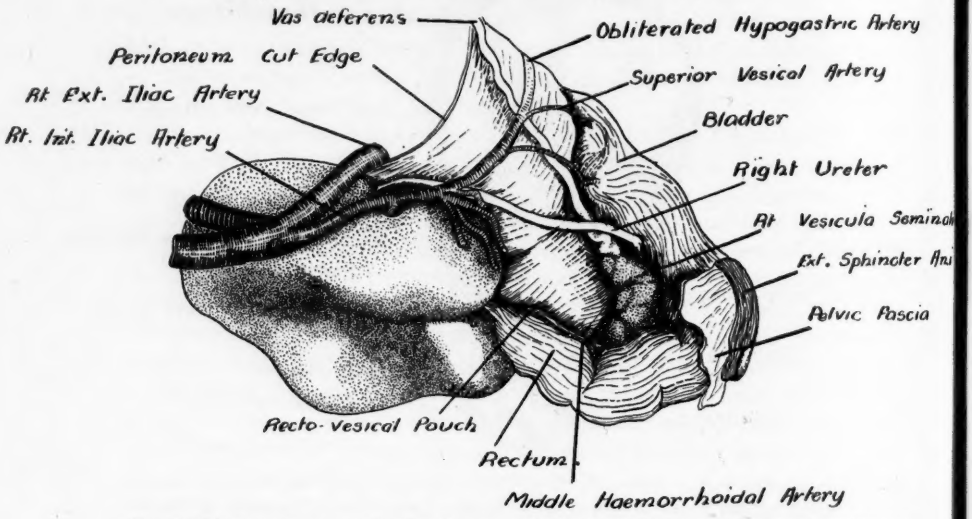

Fig. 2. This figure is a reproduction in pen and ink of a photograph. The fused renal organs with the rectum, bladder, peritoneum and adnexa *in situ* after reconstruction and dissection are shown from the right postero-lateral aspect. Explanatory annotations are given for the more prominent structures.

Approximate symmetry of the two halves of the renal organ is found in both lateral aspects. Each lobe is marked by a deep cleft which runs in a forward and downward direction, and which may be considered to subdivide the lateral lobes into right and left upper and lower lobes. These lateral clefts lodge the terminations of the common iliac arteries and the upper parts of the internal iliac arteries. The external iliac arteries leave the upper ends of the lateral clefts and proceed forward by the sides of the upper lobes.

The front of the organ is grooved in a sagittal axis though not so deeply as the back. This groove lodges blood vessels which connect with the plexus

which covers the anterior surface; see fig. 5 which also shows the ureters arising from the middle of the front of the organ and from the lateral clefts.

THE URETERS

Fig. 3 represents an outline drawing to scale of the anterior aspect of the kidney, with a centimetre scale above. The prominent contours are shown in bold outline, the kidney ducts are represented in dotted outline where they are hidden from anterior view in the lateral clefts, and elsewhere in continuous double lines.

Both ureters conform to the type of "ureter fissus" or split ureter in the terminology of Kiebel and Mall (1).

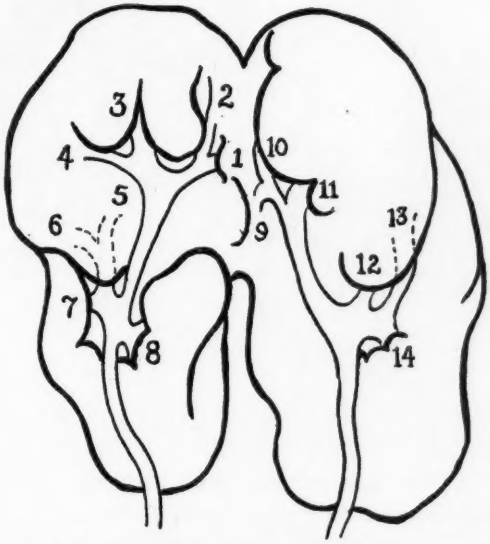

Fig. 3. This figure is an outline drawing to scale of the kidney viewed from the front after dissection to show the details of the ureters and smaller renal ducts. The prominent contours are shown in heavy black lining, the ureters and smaller ducts are in continuous lines except where hidden from anterior view, here they are dotted. Ducts numbered 1 to 4, 5 to 8, 9 to 11 and 12 to 14 represent four imperfect renal pelves.

The right ureter receives ducts from eight points which are numbered 1 to 8 in fig. 3. Most of the ducts arise from shallow clefts in the kidney, but those numbered 2 and 4 are almost flush with the kidney surface. The arrangement suggests that ducts 1, 2, 3 and 4 represent one kidney pelvis, and ducts 5, 6, 7 and 8 a second.

The left ureter receives ducts from six points, which are numbered 9 to 14

in fig. 3 and are arranged in two groups of three. Duct 9 emerges flush with the kidney surface and 13 is hidden deeply in the lateral cleft. The arrangement again suggests a fusion of two kidneys, of which ducts 9, 10 and 11 represent the pelvis of one, and ducts 12, 13 and 14 the pelvis of the second.

The right ureter measured 8·9 cm. from the point of division to the point of entry into the bladder, and the left ureter 8·3 cm., both after hardening and dissection.

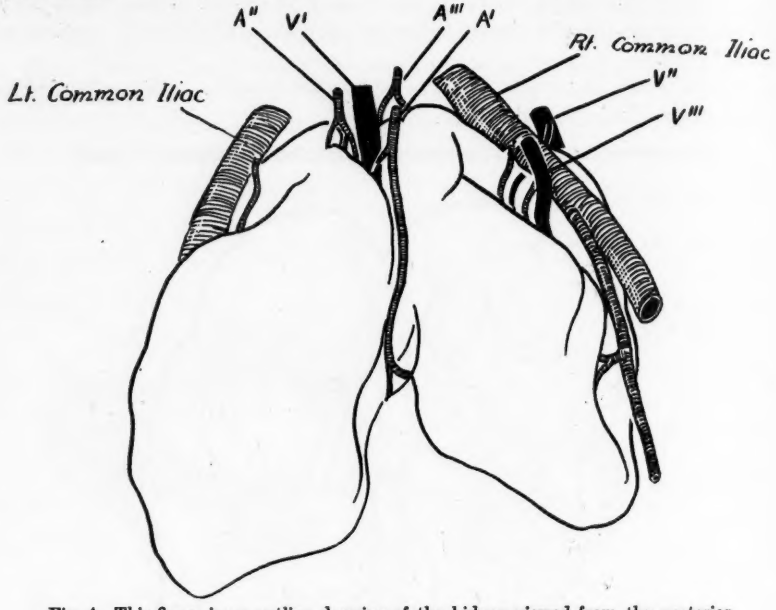

Fig. 4. This figure is an outline drawing of the kidney viewed from the posterior aspect and dissected to show the details of the blood vascular system.

BLOOD VASCULAR SYSTEM

Figs. 4 and 5 show the anterior and posterior views of the kidney drawn after dissection. The arteries are distinguished by cross lining, the veins by solid black and the kidney ducts are represented in double outline.

ARTERIES

The arterial supply is derived from the middle sacral, the common and internal iliac arteries.

Fig. 4 (posterior) shows an artery *A'* in the postero-median groove, which I identify with the middle sacral artery. At the lower end of the isthmus this vessel divides and gives one branch to the left lower kidney pelvis, and a second branch which enters the right lower kidney at some distance from its pelvis. These branches are shown in the lower median cleft, as they proceed from the back to the front of the organ, in fig. 5.

The artery *A''*, which is shown in both figs. 4 and 5 and which is a branch of the left common iliac artery, enters the left upper kidney in a small cleft, and also gives off one posterior and two anterior branches, of which one enters the left upper pelvis.

A''' is probably a branch of the right common iliac artery. One branch enters the upper pole and a second the pelvis of the right upper kidney.

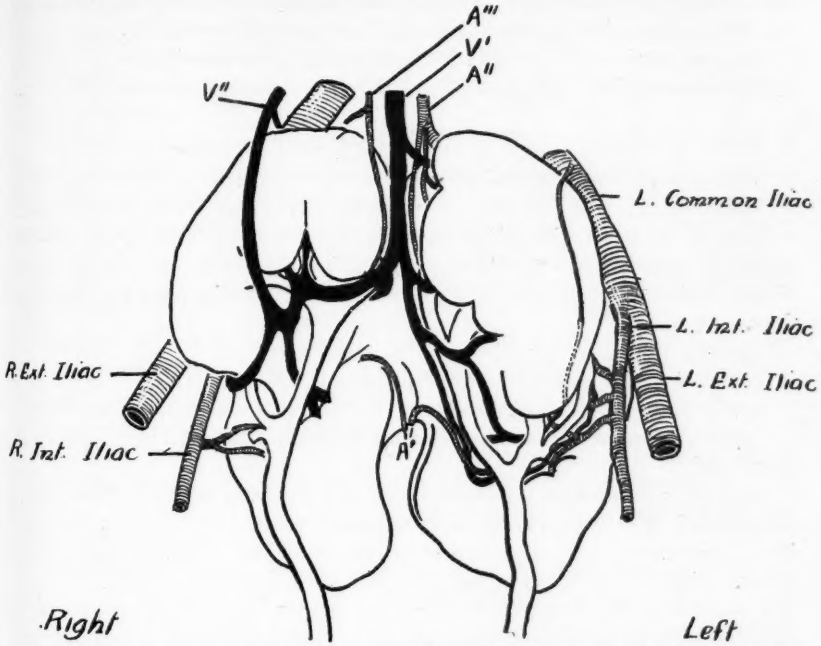

Fig. 5. This figure is an outline drawing of the kidney viewed from the anterior aspect after dissection to show the details of the blood vascular system. The arteries are represented in cross lining, the veins in continuous black and the ureters in double lines.

The lower kidneys are mainly supplied by the internal iliac arteries. The right lateral cleft contains two branches from the right common iliac and two from the right internal iliac artery, the last of which enters the right lower kidney pelvis. The left lateral cleft lodges four branches from the left internal iliac artery which enter the left lower pelvis. A twig from the left common iliac artery seems to be directed to the left lower pelvis across the front of the organ, but its continuity is destroyed.

VEINS

There is no correspondence between the arteries and the veins. Three veins drain the kidney, which are indicated by *V'*, *V''* and *V'''* in figs. 4 and 5.

Fig. 5 sufficiently shows the position and intercommunications of V' and V'', which lie on the anterior surface.

V''', shown in fig. 4, emerges from the upper part of the right lateral cleft posterior to the right common iliac artery and apparently drains the right lower kidney.

The channels of venous drainage for the left kidney seem inadequate compared with those for the right kidney. There seems no outlet for the plexus in the left lower pelvis other than the vessel communicating with V'.

I am uncertain of the termination of these veins, but surmise that V' enters the left common iliac, and that V'' and V''' enter the right common iliac vein.

DISCUSSION

The arrangement of the kidney ducts strongly suggests the presence of two imperfect renal pelves and two fused kidneys, upper and lower, on each side.

There is no duplication of the ureters at the lower ends and the bladder is perfectly normal. This suggests that duplication has taken place in the early kidney rudiments rather than in the ureteric buds that arise from the Wolffian duct.

It seems probable that this condition arose

(1) by a caudal and cranial duplication of the metanephros;

(2) by fusion of the upper and lower metanephros elements of each side;

(3) by fusion between the two upper metanephros elements in the mid-line of the body.

In Gray's *Anatomy* (2) a reconstruction of a 7 mm. embryo by Prof. Peter Thompson is reproduced; in this figure a kidney rudiment is represented lying in the angle between the dorsal aorta and the umbilical artery, tailward of the latter. Kiebel and Mall (3) represent a like condition in a 5·3 mm. embryo. The position of the lower kidneys in my specimen corresponds exactly to a retention of this early developmental stage. What influences determine the persistence of this stage can only be conjectured. Perhaps fusion at the cranial end and apposition to the bifurcation of the aorta are responsible.

Horseshoe kidney as usually met with differs from my specimen in other respects besides ectopia.

(1) Horseshoe kidneys seldom exhibit multiplicity of kidney elements.

(2) The isthmus of a horseshoe kidney rarely is situated at the upper pole.

McFarland (4) refers to the observations of Beyer (5) who noted that the isthmus occurred at the upper pole in 18 out of 262 specimens of horseshoe kidney, i.e. in 7·85 per cent. My specimen, then, is a rare one, even if it is regarded only as a variant of horseshoe kidney.

McFarland quotes Rokitansky (6) in discussing the factors that determine the position of a horseshoe kidney. "The more complete the fusion, the lower is the position of the kidneys. The completely fused mass is commonly situated at the promontory or even at the concavity of the sacrum... the fusion prevents the complete rotation of the kidney on its vertical axis, leaving the

pelvis facing anteriorly. The posterior surface of the kidneys is usually smooth, quite in contrast with the curiously retained fetal lobulations on the anterior surface."

These generalisations of Rokitansky are of interest. In my specimen the fusion of the two upper kidneys is almost complete, rotation has been arrested and the pelves face anteriorly. The pelves of the lower kidneys face laterally, which suggests that their rotation has been arrested at a stage earlier than that of the upper kidneys. The position of the fused kidneys on the sacral promontory bears out the views of Rokitansky.

Neither the anterior nor the posterior surfaces present the appearance of foetal lobulation.

Keith (7) remarks that the upper lip of the hilum is usually lacking in a horseshoe kidney. In this specimen it is noted that in addition to imperfect formation of the hilum, especially in upper kidneys, certain of the kidney ducts open flush with the kidney surface, as is shown in fig. 4.

The normal arrangement of the blood vessels and of the ureter in the renal pelvis has completely broken down. The blood supply is derived from the nearest local source.

It seems probable that it would have been possible to palpate this kidney *per rectum*. The distance from the external sphincter to the lowest point of the kidney measured 6·6 cm. or $2\frac{5}{8}$ in. Dr Strachan expressed no doubt that the kidney would have been palpable *per rectum*.

Considering the intimate relation of the kidney to the bifurcation of the aorta and to the two common iliac arteries, it is a justifiable speculation that the organ would have transmitted pulsation from the great arterial trunks to the examining finger.

Ureteral catheterisation would have revealed the shortness of the ureters. A pyelogram would, I am confident, have given a shadow with a form very similar to the outline in fig. 3. Post-mortem pyelogram was impracticable owing to the incisions in the kidney.

POST-MORTEM OBSERVATIONS ON THE INCIDENCE OF CONGENITAL ABNORMALITIES OF THE KIDNEY

Dr Sutherland Strachan has very kindly furnished a short statistical summary of the congenital abnormalities of the kidney observed in the post-mortem room of the Johannesburg General Hospital from the beginning of 1925 to May 1928.

During this period the following post-mortem examinations have been performed:

Europeans	488
Natives	839
Eurafricans	137

The following abnormalities have been found:

Europeans.

(1) Absence of the left kidney—male, aet. 51.
(2) Absence of the left kidney—male, aet. 52.
(3) Horseshoe kidney—male, *circa* 50.

Natives.

(1) Absence of the left kidney—female, aet. 60.
(2) Absence of the left kidney—female, aet. 12.
(3) Multiple kidneys, ectopia and fusion—male, aet. 30 (case described).
(4) Ectopia of right kidney, position in pelvis—male, aet. 30.

Eurafricans.

(1) Absence of right kidney associated with congenital atresia of the bile ducts—aet. $1\frac{3}{4}$ years.

The proportional incidence of congenital abnormality of the kidney observed by Dr Strachan is as follows: Europeans, 3 out of 488; Natives, 4 out of 839; Eurafricans, 1 out of 137. It is impossible to infer that one race is more prone than another to congenital abnormalities of the kidney.

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NOTES ON A FEMALE LLAMA[1]

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THE llama, a native of Peru and Chili in South America, while sharing with the camels the presence of canine teeth in each jaw, and a pair of small incisors in the upper, an aberrant ruminant stomach, and in wanting the hind toes common to other members of the order, differs from them (1) in having the toes separated, whereas in the camels they are united by a pad-like sole; (2) in the absence of humps on the back; (3) in the absence of the first canine-like molars of the lower jaw. The hair of the llama too is long and suited for protecting it on the cold mountains. The toes are furnished with nail-like hoofs, pointed and ridged on the upper side. The structure of the foot, while unfitting the llama for travelling with ease on sandy flats, is admirably adapted for scrambling over rocks and down steep slopes. Its colour is generally light brown with pale patches, and the height of the shoulder is about 3 feet, but the long neck, being mostly carried erect, bears the head nearly 5 feet from the ground. In South America it is quite domesticated, the males, at the age of 4 years being trained to carry burdens, while the females are kept at pasture in the mountains. They are chiefly employed in the silver mines of North Peru, where, from the security of their footing, they prove of much service in carrying the ore down rocky slopes. Like the camels, when they find themselves too heavily loaded, they lie down, and no effort will raise them until part of their burden is removed. Tschudi, a traveller, who, together with Darwin and, more recently, R. O. Cunningham, threw much light on their habits, states that the burden should not exceed 125 lb., and that the ordinary loads are seldom above a hundredweight. They are frequently taken in large flocks to the sea by the Indians for the purpose of bearing back salt, travelling from 10 to 12 miles a day, and graze as they go, or during a halt, as they do not feed at night. The keeping of a herd of llamas is stated to be a matter of little difficulty; at night they are put in an enclosure, where they sleep—winter and summer—without shelter, although at the elevation they generally inhabit the temperature often falls below freezing-point immediately after sunset—even in summer. In the morning they are allowed to quit the enclosure and forage for themselves—returning again in the evening of their own accord. Their flesh,

[1] The distinguished author of this paper, Prof. Carmichael McIntosh, was born at St Andrews, Scotland, on Oct. 10th, 1838. As he explains in his introduction his dissections were made and this paper was originally written in 1862; it is now brought up to date and published for the first time. Prof. McIntosh was a pupil of John Goodsir. (Editor.)

milk, skins and wool are all valuable to the owners. From their comparative hardihood acclimatisation in this country, Scotland more especially, would not seem to be difficult. A warm climate is adverse to their constitution and habits, and, even in Peru, when the natives take them from the heights to the coasts, many perish in the lower and warmer regions on the march.

The opportunity of examining, in 1862, an adult female llama I owe to the late Dr Fraser Thomson of Perth and Mr D. Lumsden of Pitcairn-green, near Perth. The latter had purchased a male and female in London in August and placed them in his park, but the male seldom suffered the female to be at rest, and it was thought that such incessant sexual excitement had hastened the death of the female in November. In these gregarious animals the females greatly exceed the males in number, and thus the attentions of the latter are widely distributed. Be this as it may, the number and extent of the bruises on the neck and trunk of the carcass proved that it had been subjected to considerable violence by knocking against fences and the rails of its enclosure. The front of the neck and its lower part was one continuous seat of ecchymosed cellular tissue, a likely place for such injury under the circumstances. The muscles were well coloured except at the ecchymosed portions, and the appearance generally belied the account given by some that it is unpalatable.

The depth of the chest was great, but it was at the same time narrow and flat. On opening the abdomen a quantity of opaque serous fluid escaped, in which broken pus cells, granules and altered blood-corpuscles occurred. The intestines—especially in and near the pelvis—manifested signs of inflammation, the mesentery showing here and there areas of reddened and thickened tissue. Fat was scattered on the omentum in small nodular masses mingled with shreds and patches of lymph; the coats of the intestine were very thin, and, from the gluing of the serous surfaces in many parts, lacerations in removal took place.

The liver was somewhat pale and marked by several digitations and irregularities on the left side. When the finger was passed over the surface, on either aspect, numerous hardened masses were felt; these were generally indicated by a lighter tint, and varied in size from a pea upward. When one of the largest was cut, it presented a somewhat dense cheese-like structure and was friable. Microscopically the tissue was cellular, many of the cells being compound and containing smaller, nucleated cells in their interior—like cancer cells. Almost all the simple cells contained a clear and distinct nucleus of some size. There were also a few caudate cells. These morbid growths occurred throughout the liver and several reached the size of a small apple. The extreme breadth of the liver was 16 in. and the depth 11 in.

The paunch was well distended. At the oesophageal opening, in the diaphragm, a slight rupture of the wall had occurred, so that extravasation of a little fluid had taken place, probably, however, post-mortem. The paunch held a great quantity of grass—fine and coarse—numerous fragments of leaves,

a few seeds of barley and some hairs. The second stomach (reticulum) contained comminuted food, whilst the third and fourth also had comminuted grass, and several angular stones. The stomach agrees with that of the camel in being devoid of the "maniplies" and thus differing from that of the ordinary ruminant, and presenting other interesting peculiarities. Before removing the food from the paunch it was seen that the usual rows of bullae covered a considerable portion of the surface—the walls being of a thinner nature than the rest of the organ, their contents giving the rows a dark bluish aspect. Two sets of these occurred, the larger deep and broad, the smaller elongated and narrow.

Before entering into the anatomy of the organ the views of the earlier authors may be alluded to. Thus Pliny (1) observes "that the camels are without upper rows of teeth, like oxen they carry burdens, and can sustain thirst for four days. They then fill themselves full enough for the past and the present. Moreover, before drinking they trample the water, otherwise they take no pleasure in drinking." Dr Derham (2) states, "The peculiar contrivance in the dromedary or camel's stomach is very remarkable—which I will give from the Parisian anatomists. At the top of the second of the four ventricles there are several square holes which are the orifices of about thirty cavities, made like sacs placed between the two membranes, and do compose the substance of this ventricle. The view of these sacs made us to think that they might well be reservatories, where Pliny saith that camels do a long time keep the water which they drink in great abundance to supply the wants thereof in the dry deserts." Daubenton's (3) account of the stomach of the llama was fairly satisfactory.

Again, only general remarks or suggestions as to acclimatisation in France and other continental countries were made by Klaproth (4), Perrault (15), Hamilton (17) Traill (18), Dawson (20), Stannius (21)—teeth, Bonafous (24) Castelnau (25), St Hilaire (26), Deville (27), Girondet (28), Roehn (29), Wisse (30), Masters (35), Thomas (37), and Prichard (39).

W. J. Walton (5) gives the stomach (ventricles) four coats. The paunch contains undigested food, is thick in the huanoco, and has bezoar stones with a nucleus of flint. The second ventricle is muscular and reticulated. He does not think it and the former act as reservoirs but that their fibres, excited and agitated by the presence of aliments, move with the aid of the diaphragm, successively in opposite directions, and roll, mix and attenuate whatever is enclosed within them. He seemed to follow Père Feuillée's observations; and adds that copulation takes place with the female on her knees.

Leuckart (9) in reviewing Molina showed that *Equus bisulcus* (*Auchenia*) belonged to the Camelidae. C. Christen (10) refers to various representatives, viz. vicugna, llama, paco and guanaco, pointing out that the largest subglobular stomach is the *rumen*, containing cells, and the second the *reticulum*, also cellular. He shows the differences between these and the stomachs of ordinary ruminants, and gives the general physiology of the parts in con-

nection with the views of others who discuss the question of the storage of water.

A careful account of the llama's stomach was given by Dr Robert Knox (11) with three plates. He described the paunch as having "a partly smooth mucous surface and partly with rows of cells. This communicates with the second stomach by an aperture which admits the hand, and the surface of which is entirely composed of cells—less deep than those of the paunch. An aperture somewhat larger than the finger leads to the small third stomach which is marked by elevations crossing each other at right angles, and occupying merely the upper part of the cavity—no contraction occurring between this and the fourth stomach. The latter is marked by about 20 longitudinal folds. Between this and the fifth stomach is a natural contraction, and its surface is covered by soft mucous membrane." He does not offer any definite opinion as to the capacity of the llama for enduring thirst, but he points out that the structure is the same as in the camel. He considers the stomach in all animals as a single organ, yet his separation of the organ in the llama into five divisions is doubtful.

Sir E. Home (14) refers to the observations of Daubenton as trustworthy, whereas Cuvier did not quote him, and he (Home) gives front and rear views of the llama's stomach. Mr Spencer (12), again, observes that the cells in the stomach of the camel contained food, and, like John Hunter, he had doubts as to their sole function being receptacles for water. Prof. Meyer (22) states that, contrary to Brandt's view, the stomach of the llama has four cavities, as the final one is really double.

A notable publication on the stomach and other internal organs of the llama was that of J. F. Brandt (23) who procured specimens from the king's menagerie at Potsdam. He treats of the lips, gums, tongue, teeth, digestive system, brain and other internal organs. He describes the paunch, reticulum and third stomach, his figure in Plate VII, however, indicating the differentiation of the latter into two divisions. He did not specially describe the functions of the valve at the duodenum, though the muscular band leading to it is shown.

Crisp (33) quotes Sir E. Home's case of a Bactrian camel which drank a large quantity of water before death, the water being found in a pure state in the cells. He describes the rumen as lined with flat epithelial cells instead of villi, and the muscular fibres which end in divisions which exercise considerable influence on the closure of the water-cells. He also mentions having found large "water-bags" in the rumen of the Saiga antelope.

Pilliet (36) gives a general description of the cells in the camel's stomach and those found in other Vertebrates.

Sir R. Owen (34) observes that "the rumen has the dense epithelial lining, but is destitute of the villi which characterise it in the horned ruminants. It is partially divided into two compartments by a strong fasciculus of muscular fibres, which, commencing at the left side of the cardiac orifice, traverses the

paunch longitudinally. On the right side of this ridge, about fourteen smaller muscular fasciculi pass off at right angles, and these ridges are connected by still smaller fasciculi, running transversely between them, at definite distances from each other; the quadrangular spaces which result from the above arrangement of fasciculi are partly closed by a production of the lining membrane leaving a circular aperture in the centre of each square for the passage of liquids into the cells beneath. The compartment of the paunch, to the left of the great longitudinal ridge, terminates in two sacculi, at what may be considered the cardiac extremity. The sacculus nearest the oesophagus is simple; the one furthest from it is developed into a series of cells, of a smaller size, but of precisely similar construction to those on the opposite side of the paunch—a series of smaller muscular bands passing off at right angles from the larger one which separates the two sacculi, and these lesser bands being connected by transverse fasciculi, in the intervals of which the cells are developed."

This description agrees for the most part with that of 1862, though Sir R. Owen keeps to the old view as to the water-cells, and apparently had not seen food therein in other examples.

The second stomach is thus described by this author: "The reticulum or water-bag shows that the cells are situated between a series of parallel muscular fasciculi, as in the rumen; but their further subdivision is carried to a greater extent, and their orifices are not guarded by membranous productions. The dense epithelium is not continued into this cavity; its muscular coat is so disposed that the exterior is smooth and uniform, and the cells are scarcely visible from without. A muscular ridge, longitudinal at the end of the oesophagus, winds round the upper part of the reticulum to terminate at the orifice of the psalterium. By the contraction of this fasciculus, all communication between the first two cavities and the oesophagus is cut off, and food is conducted to the third cavity. A slighter degree of contraction cuts off communication with the rumen, and allows the passage of fluids direct into the reticulum or water-bag, which probably takes place when the camel or llama drinks."

Sir R. Owen mentions that "the oblique canal leading to the third cavity, forms, in the camel, a small sacculus, distinct from, and intervening between, the reticulum and psalterium: it is not so distinct in the llama; but on a close inspection, the inner membrane nearest the orifice above mentioned may be seen to be produced into ridges which are arranged in a reticulate or alveolar form; and as a similar structure is more distinctly observable in the camel, this cavity was considered by Daubenton as the homologue of the reticulum, and the water-bag as a peculiar superaddition. The remainder of the stomach forms one continuous cavity, bent upon itself at its lower third—without rugae or laminae, the latter being afterwards developed at the cardiac half of this cavity. The pylorus is a small transverse aperture, protected above by a large oval protuberance. The duodenum is considerably dilated at its commencement." He mentions that "the muscular longitudinal fasciculi between the cells are less thick than those in the paunch, and that the middle fibres

in each become tendinous (in the llama), the transverse fasciculi continue muscular."

Sir William Flower and Lydekker(38) observe that the paunch has no villi on its surface, and that there is no distinct psalterium. Both the first and second compartments have a number of pouches or cells in their walls, with muscular septa and a sphincter-like arrangement of their orifices by which they can be shut off from the rest of the cavity, and into which the fluid portion only of the contents enters.

Milne Edwards(32) observes that "the camel is exceedingly temperate in the use of water, a quality which has been ascribed to the peculiar form of its stomach; in two of these are large cells which either serve as reservoirs or which have the power of secreting water," adding that the llama especially resembles the camel in the structure of its stomach.

Dr Carpenter(31) states that it is in the reticulum that we find the arrangement of water-cells in the camel, by which it is enabled to retain a supply of water for several days. The cells are nothing else than the little pits seen in the honeycomb stomach of the sheep, though they are deeper, and each may be closed at the top by the contraction of the muscular fibres at its orifice.

Unfortunately the fine example of the stomach of the female llama in the University has been lost since my retirement, but several interesting preparations occur in the museum of the Royal College of Surgeons, London. The first of these is the stomach of a foetal llama (J. 811. 1), in which the rumen is marked externally by about fifteen rows of transversely divided loculi. The description in the catalogue is nearly as follows: "The oesophagus has been cut open to show two muscular ridges bounding a furrow winding round the anterior (oral) wall of the reticulum to the passage to the psalterium, and forming, when opposed, a direct passage to the third stomach. It is obvious that by the contraction of these fasciculi all communication between the first and second cavities would be cut off, and the re-masticated food, as in the ordinary ruminant, would pass into the third cavity. A slighter degree of contraction would cut off the communication with the rumen and allow passage of fluids direct into the reticulum or water-bag....A free communication, however, exists between the latter and the paunch." "A porcupine's quill has been passed through the oblique canal leading to the third cavity." "In the llama, on close inspection, the inner membrane nearest the orifice just mentioned is produced into ridges which have a reticulated or alveolar form." "The pylorus is a transverse aperture protected, as in the pigs, by a large protuberance. The commencement of the duodenum is considerably dilated."

Preparation J. 811. 2 (llama) shows the gutter bordered by two muscular ridges which leads from the oesophagus to the rumen and psalterium. A portion of the greater group of cells in the left region of the rumen is shown in J. 811. 3 (llama), and it is stated that, after death, the smaller matters, as

grains of oats, may pass into the cells, but their contents are always found to be chiefly fluid. Preparation J. 811. 4 shows the reticulum or "water-bag" of an adult llama, covered by columnar and glandular epithelium and minute papillae. The crest in two of the muscular ridges has been replaced by tendon. None of these becomes tendinous in the camel. The external layer of muscle has been exposed on the reverse of the reticulum.

Portions of the rudimentary psalterium and abomasus are mounted in J. 811. 5, and the two parts depend for their distinction rather upon the disposition of the lining membrane than upon any natural constriction. In the psalterium the lining membrane is raised into a series of low, parallel. wavy laminae, whereas in the abomasus it is smooth or slightly villous. It is to be noticed that in the foetal llama the psalterium is not laminate.

A comparison between this laminate part and that of the ox (J. 828. 1) raises doubt as to the value of the foregoing distinction. It seems probable that the psalterium is absent in the Camelidae, and that the laminae just described belong to the true digestive stomach, and are comparable to the laminae in the commencement of the abomasus in the ox.

The pylorus of a llama in J. 811. 6 "has its valvular plug bisected so as to show its spongy texture. It is composed of submucous cellular tissue, the cells being large and filled with fluid, and thus the parts are rendered elastic. No glandular follicles are observable, nor any conspicuous orifices in the mucous membrane covering the protuberance, yet it has been called glandular. The office of the valve would appear to be to allow the passage of sufficiently comminuted and digested food, and to arrest that of undigested matter."

On comparing the llama's stomach with that of the sheep, the entire absence of the fringe-like processes in the paunch of the llama is noteworthy, for the cavity is everywhere lined by smooth mucous membrane. A greater difference, however, lies in the presence in the llama of the two series of membranous and muscular sacs noted previously. Slanting down from the opening of the oesophagus on the right side is a strong muscular ridge measuring about a foot in length, and giving origin, throughout part of its extent, to a series of smaller, but yet powerful parallel transverse muscular bands, which, proceeding for a considerable distance, gradually fade into the ordinary muscular coats of the stomach. Between these bands are situated the rows of cells above mentioned. The first row of the larger series commences with an irregular number of cells; in the rest of the septa the cells are generally arranged in a double row. In the former there are superficially a series of strong musculo-membranous septa—mostly transverse—and, below the level of these, are others which subdivide the major divisions of the former into smaller compartments each more or less steadied by attachment to the nearest parallel muscular band. These bands, increased in strength from before backward, lay above, and seemed to have a special action on the stomach-cells. The cells were filled with the ordinary contents of the paunch, though the food was softer and more moist, but not more masticated than that in the general cavity,

since coarse fragments of grass and leaves were plentiful. The number of the parallel muscular bands is thirteen, being five more than Sir E. Home found in the stomach of the camel. The other elongated patch of cells has thirteen septa and seventeen well-marked rows of small cells, having a similar arrangement of membranous septa to the foregoing, and being likewise filled with the moist though ordinary contents of the paunch.

The second stomach (reticulum) of the llama opens by a somewhat wide aperture into the former, which aperture, however, can be closed by muscular action. Instead of the superficial honeycomb arrangement of the ordinary ruminant stomach, a number of deep cells of large dimensions, connected with a series of transverse septa which are divided and subdivided in all directions, are met with. These also contained some finely triturated food, and were not entirely empty, as is asserted in regard to this division in the camel, but this might have been accidental, since Daubenton termed it a reservoir. The smooth surface commencing at the oesophagus and running to the next division is proportionally larger than in other ruminants and less defined.

The psalterium, as indicated, is absent, at least as a "maniplies."

Beginning at first by a smooth mucous surface, the next region shows by-and-by an elongated and longitudinally ribbed condition for the distance of a foot (supposed psalterium?); then, at a well-marked line, the ridges cease, and a smooth villous surface clothes the rest to the pylorus. A little posterior to the termination of the ridges is the margin of a very powerful transverse muscular band which partially divides this portion into two compartments (designated by Cuvier and others separate stomachs in the camel), the posterior or pyloric division sending a process forward below this transverse muscular ridge. The pyloric division is marked by fine rugae and has the muscular elements much increased. The pyloric aperture is crescentic—with the hollow forward—and the space is occupied by a prominent more or less muscular "boss," stated by Home to be glandular in the camel, which completely blocks the aperture when *in situ*. This "boss" is the massive more or less glandular termination of a strong muscular band which comes all the way from the second stomach, while the muscular band resulting from the junction of the two halves of the crescent goes but a short way on the opposite wall. It will thus be seen that the contraction of the former muscle will materially influence the entire stomach as well as affect the pyloric aperture.

The intestine begins a little below the "boss" and runs up for 2 in. above the external margin of the crescent.

The physiology of digestion in the llama would seem to be much the same as that in the camel, though the importance of the second stomach has been somewhat exaggerated in relation to water-storing qualities, the more so in the case of the present animal, the habitation of which is not amid arid deserts, but near great mountains where moisture is not scarce. Moreover, as previously mentioned, heat and fatigue, the circumstances in which a store of water would be of most value, are found to be inimical to the well-being of the animal.

Having cropped the grass it passes into the paunch, where, by the muscular movements of the walls, it becomes thoroughly mixed with such secretions as it contains, and part, portion by portion, is lodged in the various cells between the muscular septa in which a further pouring forth of gastric secretion is combined with the rounded pellets, so that it is easy, when pressed out of the general as well as the cell-cavity, for it to proceed by muscular contraction to the oesophagus and mouth. After thorough mastication it passes again down the oesophagus to the second stomach and perhaps part to the third in a condition which affects certain nerves of the region, the muscles supplied by which are kept rigidly contracted. John Hunter likewise considered that it entered the second stomach, as in other ruminants, but Home denied this, averring that only water entered this peculiarly developed organ. Unless the muscles concerned are under the control of the animal, which Milne Edwards and others say they are not, then the nerves of the parts have a difficult task in distinguishing between water and what is almost as fluid.

The food then arrives in the combined third and fourth stomachs where digestion is thoroughly carried out before any is allowed to pass the strongly guarded pylorus.

The next organ specially examined was the bi-horned uterus and its appendages. When *in situ* the ovaries were conspicuous—hanging like tuberculated nodules attached to the broad ligament. All the pelvic organs were marked by traces of vascular excitement, the bladder being reddened from congestion. The vagina was relaxed but not inflamed, its surface having numerous cells of the ordinary epithelial character, but no spermatozoa could be detected even close to the *os*. The latter was open, and marked by a finely crenate margin, which, with the entire cervix, was injected and covered with tenacious mucus containing cylindrical epithelium and many spermatozoa, and it is possible that the male organ extended thus far *in coitu*. The same microscopical structure was met with throughout the region along with oval blood-discs, which were larger than the head of a spermatozoon. The cervix was marked by rough grooves and striae and had a dark colour when the mucus was removed from its surface. Towards the base of the left cornu of the uterus the usual cylindrical epithelium occurred, but no perfect spermatozoa, though bodies resembling heads appeared in the fine granular matter. At the extremity of the cornu large and small oil-globules were evident, with the débris of a ruptured ovum, resembling the albuminous fragments in the vagina. At the extremity of this cornu, just at the entrance of the Fallopian tube, was a deeply congested portion of the membrane with the pouting end of the Fallopian tube in the centre. Over this portion the rounded, granular epithelial cells were much smaller, and the free granular elements more abundant. The right cornu offered nothing worthy of note. The posterior or dorsal surface of the uterus was much marked by contorted vessels—chiefly veins.

The left ovary was the larger, and contained many (eight or ten) *corpora lutea*; the smaller, right, was rounded and had a projecting Graafian vesicle

with an ovum in the centre. On section the dark bluish grey *corpora lutea* were dense, in some cases without any central differentiation, whilst in others a regular concentric arrangement surrounded a paler central portion[1].

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[1] Unfortunately, reference to the well-preserved specimens of the foregoing organs of the llama was rendered impossible by their disappearance from the University Collection after the author's retirement in October, 1917.

ANATOMICAL NOTE

AN ABNORMAL LEFT BRONCHIAL ARTERY

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THE bronchial arteries correspond to splanchnic arteries and represent their continuation to diverticula of the gut. The usual origin of the right vessel from the first aortic intercostal artery must result from the enlargement of an anastomosis between a splanchnic vessel and the first part of an intersegmental somatic vessel; the anastomosis is much less frequently developed on the left side, and when it is developed it is much more often the lower than the upper vessel which arises from the intercostal series (see the analysis of the origin of the bronchial arteries by Nakamura, *Anat. Anz.* Bd. LVIII, S. 508, 1924). The origin of a single left vessel from the left subclavian artery has been described (Turner, *Trans. Med.-Chir. Soc.* vol. XXX, 1862), but it is extremely infrequent, and though the subclavian arteries are usually mentioned as an aberrant origin for the bronchial arteries it is apparently always Haller's case which is recorded (Quain, Rauber-Kopsch, Power, etc.), and that example differs from the one recorded here in being the origin of a combined trunk for the right and left bronchial arteries. (T. W.)

IN a male subject, aet. 64 years, an abnormal left bronchial artery was found to arise from the postero-medial aspect of the left subclavian artery just beyond its origin from the arch of the aorta. It measures 1·5 mm. in diameter, and is unaccompanied by veins. From its origin the vessel curves round the medial side of the subclavian artery and passes obliquely downwards and lateralwards over the arch of the aorta; at the lower border of the arch it passes through some lymph glands to which it gives branches, and then winds round behind the left pulmonary artery to reach the left bronchus, behind which it enters the substance of the lung. In passing over the arch of the aorta it is crossed by the left superior intercostal vein. It is also crossed at its beginning by the left phrenic nerve, and just before it passes beneath the pulmonary artery it is crossed by the left recurrent laryngeal nerve. There was no other bronchial artery to the left lung. It gives off numerous branches in its course; at its origin several twigs pass to the oesophagus and trachea; as it crosses the aortic arch numerous small branches from it ramify on the aortic wall; and below the aorta it supplies branches to the lymph glands.

OBITUARY NOTICE

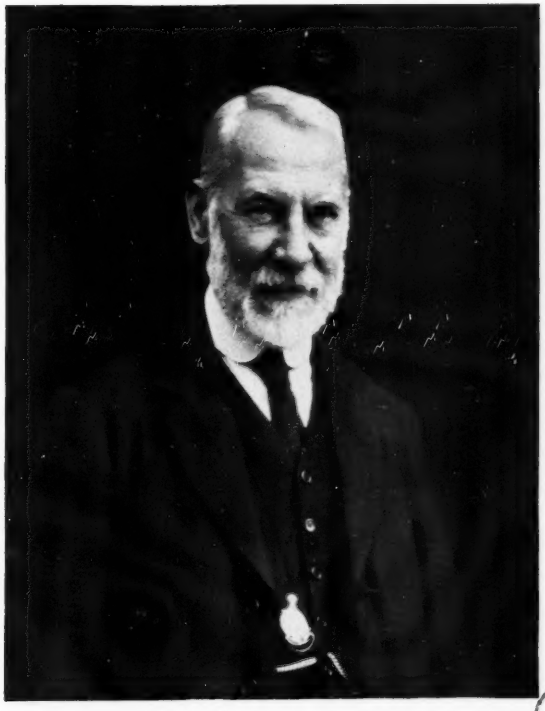
SIR GEORGE DANCER THANE

Sir George Dancer Thane died of heart failure on January 14 within four months of the eightieth anniversary of his birth. He was associated with University College, London, successively as student, demonstrator, professor of anatomy, and emeritus professor for more than sixty-three years.

The mere enumeration of the forty-nine years, seven as demonstrator and forty-two as professor, which Thane devoted to the teaching of anatomy at University College represents only one aspect of the great services he rendered. Nor did the work of research and teaching form the major element in his whole-hearted devotion to University College and to anatomy. His greatest achievement was his cultivation of a personal knowledge of every student who worked under him, and of a sincere interest in their welfare, which he maintained throughout their subsequent careers. Thus his genial personality, and in particular his passion for accuracy in observation and restraint in expressing what he saw, influenced the lives of thousands of medical men and women. This played a large part in building up the solid reputation of medical education in London.

He was born at Great Berkhamsted, Herts, on May 27th, 1850, and was the eldest son of G. D. Thane, M.D. He entered University College in 1867. Amongst his contemporaries were H. Newell Martin, who introduced British methods of biology at the Johns Hopkins University; Sir John Williams, the obstetrician; Sir William Gowers, the neurologist; Sir John Tweedy, the ophthalmologist; and Sir Rickman John Godlee, the surgeon. Immediately junior to him were Sir Henry Morris, the surgeon; Sir Ray Lankester, biologist; Sir Thomas Barlow, physician; and Sir Edward Sharpey-Schafer, physiologist. The late Sir Dawson Williams, Sir Frederick Mott, and Sir Victor Horsley were enrolled before 1874, and were taught their anatomy by Thane, who had been appointed demonstrator by Professor George Viner Ellis in 1870, a year before he obtained the diploma of M.R.C.S. He succeeded Ellis in 1877, at the early age of 27, and continued in the Chair of Anatomy until 1919, when he was elected Emeritus Professor. He was knighted in 1919 for his services to medical education in London and as inspector under the Vivisection Act of 1876.

Sir George occupied a distinguished position among British and Continental anatomists. He was one of the founders of the Anatomical Society of Great Britain and Ireland of which he was President in 1896 and 1897. He was a member of the French and German societies, and foreign corresponding member of the Anthropological Society of Paris. Forty years before Thane's



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appointment to the Chair of Anatomy, William Sharpey was appointed Professor of Anatomy and Physiology at a time when Richard Quain held the Chair of Practical Anatomy and served as Surgeon to University College Hospital. Sharpey inaugurated for the first time in England a course of instruction in microscopic anatomy, and re-edited the first edition of Jones Quain's *Anatomy*, with Richard Quain as co-editor. He introduced into this book the results of his researches in microscopic anatomy, and especially his original observations on bone. He instituted a lectureship in practical physiology "with a view to supplying medical students with instructions in the use of the microscope in examining the textures and fluids of the bodies." Thus the teaching of histology and neurology was transferred to the newly created department of physiology, and the department of anatomy was left with no equipment beyond the dissecting room, and sank to be the mere handmaid of surgery.

Thane was placed in charge of a department which was not only bereft of some of the chief interests of anatomy but also was obscured by the brilliance of the school of physiology, created by Sharpey, Michael Foster and Burdon-Sanderson, which attracted men like Schäfer, W. H. Gaskell, Gotch, Halliburton, Benjamin Moore, Leonard Hill, Bayliss and Starling. This vigorous school of physiology lured back from the hospital to the laboratories such men as Sydney Ringer, Oliver, Rose Bradford, Beevor, J. H. Parsons, and Page May. The wave of enthusiasm for physiology at this time attracted the more enterprising students and threatened to sterilise most departments of anatomy. Yet Thane managed to provide the clinical and pathological staff of the hospital with a succession of young men trained to think anatomically. His demonstrators included Rickman Godlee, Silcock, Bilton Pollard, Rose Bradford, Percy Flemming, Raymond Johnson, Mower White, George Blacker, S. G. Shattock, C. Stonham, T. W. P. Lawrence, Donald Armour, Batty Shaw, Wilfred Trotter, A. M. H. Gray, E. K. Martin, and G. S. Hett. Sir Arthur Keith worked for a time in his department.

Thane was no transcendental anatomist. He refused to pretend to be a morphologist or physiologist. His mind was content with that conception of anatomy which satisfied Claude Bernard:

"Anatomy is the basis necessary to all medical investigation, whether theoretical or practical. Anatomy in itself is a sterile science; its existence is justified only by the presence of living men and animals, well and sick, and by its own possible usefulness to physiology and pathology....Anatomy is the necessary foundation of physiology, and never can we become good physiologists if we are not first deeply versed in anatomical studies and trained in anatomical dissections."

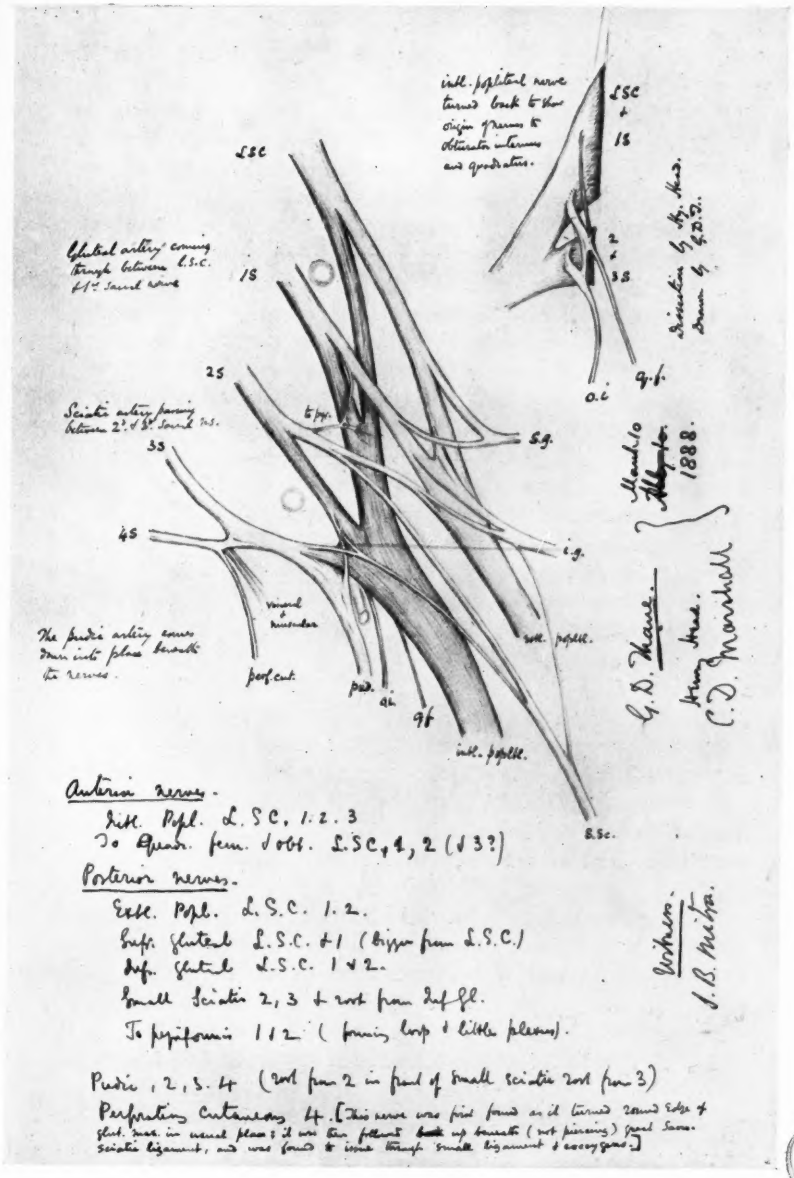
Poetic and philosophical intrusions into the domain of precise and accurate descriptive anatomy he abhorred, and he scoffed at loose analogy or fantastic simile. Although he was on terms of intimate friendship with the biometricians and displayed a keen curiosity and interest in their attempts to solve bio-

logical problems, he distrusted the statistical method, and maintained that the higher mathematics was but a form of intellectual shorthand which contributed nothing to the sum total of anatomical knowledge.

As most of his predecessors' contributions to anatomy and histology were incorporated in the various editions of Quain's *Anatomy*, so Thane's original observations are incorporated in the ninth and tenth editions of the same book, with Sharpey-Schafer as co-editor. The tenth edition of "Quain" furnishes the highest standard of precise, naked, and concentrated anatomical truth. The brevity is classical: not a redundant word or phrase: no tolerance of "it is almost universally accepted"; "there is every reason"; "it is safe to assume"; "it is tempting to suppose"; "probably each"; "presumably." On one occasion Thane said that "any fool is perfectly at liberty to assume anything he likes, but it is very much open to question whether it is safe to assume anything when considering so intricate a subject as the central nervous system." The illustrations of the bones of the skeleton in the tenth edition of Quain's *Anatomy*, from drawings by two of his demonstrators, T. W. P. Lawrence and D. Gunn, are the most accurate osteological drawings extant, and represent the highest standard of the woodcut in anatomical illustration. Thane's drawings of the small bones have been widely copied. He was an accomplished draughtsman and took a keen interest in teaching anatomy to students of art in the Slade School.

The influence of Quain's *Anatomy* was world wide. A translation of the seventh edition was published in German by Hoffmann in 1870. The translation was an immediate success. Schwalbe, not satisfied with a mere translation of the second volume, dealing in particular with the nervous system, more than doubled its size by additions. The Hoffmann-Schwalbe translation next served as the basis of Rauber's *Lehrbuch der Anatomie des Menschen* and of Schwalbe's *Neurologie der Menschen*—with no reference to "Quain." By 1920 eleven editions of Rauber's *Lehrbuch* had appeared, mainly under the editorship of Kopsch. The Rauber-Kopsch *Lehrbuch* has been repeatedly translated into various languages. The treatise edited in France by Poirier and Charpy owed much to Quain and Rauber. There is some irony in the fact that Rauber's description of the muscles, translated from the "Quain," should have been retranslated into English as the basis of many text-books of anatomy since 1889. The time is not yet ripe for a candid history of these translations and retranslations. The practice of piracy in text-books of anatomy, both in former times and to-day, would provide an illuminating theme for an essay on human nature! Sir George had an amazingly precise knowledge of the history of such "borrowings" and could discourse in the most entertaining way on the migrations of particular diagrams and the evolution of errors.

As in the "Quain," so in Ellis's *Demonstrations of Anatomy*, which Thane edited through many editions, in brief articles to *Nature*, such as that "On the Brain of the Gorilla" (December 14th, 1876), and in the various communications to the *Proceedings* of the Anatomical Society, the same precision, brevity,


L5C
1S
2S
3S
4S
Gluteal artery coming through between L.S.C. & 1st Sacral nerve
Sciatic artery passing between 2nd & 3rd Sacral ns.
The pudic artery comes from into plane beneath the nerves.
inf. popliteal nerve turned back to show origin of nerves to Obturator internus and gemellatus.
Sciatica 5 Hy. Hosp. Sam 5 4.2.5.
Glut. inf.
Sc.
i.g.
vessel & muscular
perf. cut.
pud.
gl.
inf. popliteal.
S.Sc.
Arteries.
Inf. Popl. L.S.C. 1.2.3
To Quad. fem. Obt. L.S.C. 1, 2 (3?)
Posterior nerves.
Exter. Popl. L.S.C. 1.2.
Sup. Gluteal L.S.C. 1 (bigger from L.S.C.)
Inf. Gluteal L.S.C. 1 & 2.
Small Sciatic 2, 3 & root from Sup. Gl.
To pyriformis 1 2 (forming loop & little plexus).
Pudic 1, 2, 3, 4 (root from 2 in front of small sciatic root from 3)
Perforating Cutaneous 4. [This nerve was first found as it turned round edge of glut. max. in usual place; it was then followed back up towards (not piercing) great Sacro-sciatic ligament, and was found to come through small ligament & accompany]
Hamilton 1888.
G. D. Thane.
Hosp. Stud.
C. D. Marshall
Brithem.
J. B. Murphy.

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and careful use of words is seen. In his descriptive writings, Thane was as precise as the French anatomists, as thorough as the Germans, and displayed a higher standard of self-control and a more rigid expression of anatomical truth than either.

A concrete example will perhaps convey the best idea of Thane's conception of accuracy in anatomical observation. He made reports of the work of every student, in which he collected information concerning not only their practical work in anatomy and their academic achievements, but also the personal incidents of their social and domestic life and character. As a sample of the records he kept of work in the dissecting room a page from one of his scrap-books is reproduced here. It is concerned with a dissection made in 1888 by Henry Head of the lumbo-sacral plexus. Thane made a characteristically careful pencil sketch of the dissection, recording the date and the name of the dissector. He not only signed it himself but the dissector also, with his partner Mr C. D. Marshall, were required to sign the drawing to confirm its accuracy as a record. Not satisfied with this an independent witness was called in to corroborate its correctness and to check the enumeration of the component nerves.

When it is realised that this is merely a random sample of Thane's procedure it provides not only a testimony of his respect for accuracy but also the reason why the whole of his active life was absorbed in teaching.

Thane's knowledge of the literature and history of anatomy was probably unique. It is a real tragedy that he could never be induced to put into writing the wealth of anatomical lore he poured out in his conversation. Perhaps it may become possible to issue the card index of the history of anatomy which he spent half a century in compiling.

He had a great affection for his books, with the contents of which he had an intimate familiarity and a critical appreciation of their merits and shortcomings, which were freely recorded in marginal notes. He not only knew the books with this discriminating thoroughness, but also the personal history of their authors, and often would explain the circumstances which induced them to emphasize particular aspects of their subject and to fall into certain errors. When five years ago, after long discussions, he eventually agreed to dispose of his books to University College he insisted upon bringing them himself, two or three at a time, and taking a personal farewell of each volume and paying a tribute to its author, never forgetting to mention where he had departed from the pathway of strict accuracy.

In compiling these notes of the life-work of the great teacher whose singleness of purpose was displayed in so lofty a conception of scientific truth, I have freely used the account given by his pupil Dr H. A. Harris, whom Sir George used to visit regularly during the years of his Emeritus Professorship. For his interest in the College of which he was a living link between its founders and the present day never abated to the day of his death.

G. Elliot Smith.

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